THE ECOLOGICAL RELATIONSHIPS OF THE FOOD OF THE COLUMBIAN BLACK-TAILED DEER, *ODOCOILEUS HEMIONUS COLUMBIANUS* (RICHARDSON), IN THE COAST FOREST REGION OF SOUTHERN VANCOUVER ISLAND, BRITISH COLUMBIA

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INTRODUCTION

The present investigation of the food habits of the Columbian black-tailed or coast deer, *Odocoileus hemionus columbianus* (Richardson) was conducted for the most part on southern Vancouver Island, British Columbia during the years 1937 to 1941 inclusive.

Conifer forests dominate the vegetation of Vancouver Island except in a small area on its southeast coast. Climax forests on the extremely humid west coast consist of Sitka spruce *(Picea sitchensis)*, western hemlock *(Tsuga heterophylla)*, and western red cedar *(Thuja plicata)*. Elsewhere at low and moderate elevations climax species are the hemlock, balsam fir *(Abies grandis)* and cedar. At about 4,000 feet elevation mountain cypress *(Chamaecyparis nootkatensis)*, mountain hemlock *(Tsuga mertensiana)*, and alpine fir *(Abies amabalis)* are the dominant conifers.

Throughout most of this region the Douglas fir *(Pseudotsuga taxifolia)* is the characteristic species in forests up to about 500 years old. It is a pioneer tree species and at maturity is gradually replaced by one of the two low elevation climax communities described above.

Immediately adjoining the southeastern coast of the island the dominants are deciduous species. In the drier areas the Garry oak *(Quercus garryana)* and madrone *(Arbutus menziesii)* occur in open mixed stands that may gradually give way to mixed conifer forest. In other words this oak-madrone association may under certain conditions be an associes. In the hygric areas Oregon alder *(Alnus rubra)*, broad-leafed maple *(Acer macrophyllum)* and willows *(Salix sitchensis* and *S. scouleriana)* dominate a pioneer society that goes directly to the climax conifer forest without the transition Douglas fir period. Human invasion, except for logging is confined to this coastal area.

Throughout the entire region, there are but two major influent mammals, the coast deer *(Odocoileus hemionus columbianus)* and the white-footed mouse *(Peromyscus maniculatus)*.

Extensive logging operations have been and are being conducted in all accessible Douglas fir stands. In the main these are high-lead operations that remove or destroy every standing tree and leave behind a wilderness of debris extending over areas of many thousands of acres. Slash burning is usually compulsory so that fire almost universally follows logging in the destruction of the pre-existing biotic community.

The two animal major influents rapidly repopulate all such denuded areas and if they are present in large numbers may modify the pattern of floral regeneration so that the deciduous pioneer forest rather than the fir pioneer forest develops. They can render natural or artificial reforestation impracticable, or at the very least they can materially retard the regrowth of a commercially valuable fir forest.

Preliminary studies revealed that from the standpoint of deer the food potential of a west coast climax forest is so low that over vast areas deer are almost non-existent. Though census methods are highly inaccurate on low populations in such a forest, I arrived at an approximate figure of one deer per square mile in the west coast forest north of Jordan River and south of Port Renfrew during the winter of 1937-1938.

Highest deer concentrations are reached in parts of the regenerating logged land on the east coast of Vancouver Island. Here the average population is in the vicinity of 20 deer per square mile. In one instance on Bald Mountain Game Reserve I tallied sixty-two deer, of which at least forty-two were seen once only, on a measured area of four hundred and twenty-five acres. This was not a wintering concentration. The count was taken in mid October, 1938.

It should be stated that domestic livestock are not run on such areas and except for a small number of sheep grazing at large in the open woodland adjacent to Victoria and Sooke there is little opportunity on Vancouver Island for direct competition between deer and livestock.

For the purpose of this food study of the coast deer two areas were chosen for intensive examination (Map 1). Goldstream Summit, nineteen miles northwest of Victoria, B. C., and Bald Mountain Game Reserve on Cowichan Lake, approximately twenty miles west of Duncan, B. C. In the former
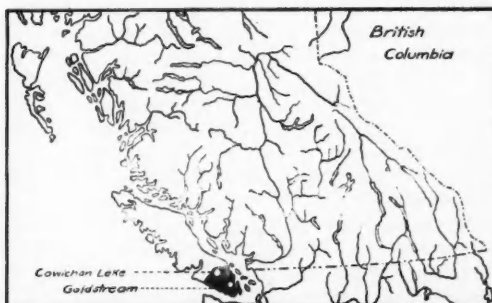
MAP 1. Map of B. C. to show location of study areas.

area deer were collected from time to time during parasite studies and these deer provided stomachs for food examination. Food studies in the Bald Mountain area were all by direct observation. From elsewhere on southern Vancouver Island deer stomachs were received through the good offices of game wardens and interested hunters.

In the extensive burned areas surrounding Cowichan Lake conditions are ideal for the study of food habits by direct observation of feeding deer. Here much time was spent watching deer with aid of a 20x telescope and by this means a considerable body of data was accumulated in terms of deer minutes (Dixon, 1934). However, examination of forage plants led to the suspicion that the conclusions as to plant species most utilized derived from watching deer feeding were not in accord with the actual conditions. That this was true was given further credence by the shooting of 3 deer after they had been observed browsing for periods of two to three hours.

By direct observation I had recorded for these deer 250 deer minutes of browsing, divided as follows: *Arbutus menziesii* 9%; *Gaultheria shallon* 23%; *Hypochaeris radicata* 45%; *Cerastium* sp. 15%; other ground vegetation including grasses 8%. Examination of stomach contents however revealed that the food of these deer in the morning browse period during which they were shot had consisted of *Pseudotsuga taxifolia* 35%; *Gaultheria shallon* 20%; *Hypochaeris radicata* 30%; *Arbutus menziesii* 10%; and miscellaneous vegetation 5%. This is at considerable variance with figures derived from direct observation which reveal no feeding upon Douglas fir.

In this area the second growth fir is concentrated at or near lake level around the lower margin of a steep rocky hill rising abruptly from the lake. The deer browsed in the fir thickets just before dawn and with the coming of daylight fed slowly up hill to their bedding grounds. The necessary confinement of direct observation of feeding deer to daylight hours led to erroneous conclusions and such observations were discontinued.

The intensive method was applied in two different ways, stomach analyses and quadrat studies of food plants.

Stomach analyses were found to yield the most satisfactory account of major food items but they are admittedly unsatisfactory as an indication of the extent of snip-browsing on a wide variety of plants.

Whenever possible stomachs were obtained from deer shot toward the end of the morning browse period. The contents of the rumen were thoroughly mixed and a sample of about a pint removed. This was washed and screened on fourteen-mesh screens. The different food species were then separated manually and the quantities of each measured by water displacement in a graduated tube.

This method gave satisfactory results with fall and winter stomachs. Admittedly certain types of food may be more finely comminuted than others and pass through the screens while other more fibrous foods do not. This source of bias was not encountered with the foods eaten on southern Vancouver Island.

Examination of spring and summer stomachs by the above method was not satisfactory. The large quantities of succulent vegetation consumed at such times becomes pulped by the water stream during screening and thus renders subsequent identification most difficult. Contents of stomachs were accordingly emptied into shallow enamel trays, flooded with water, the fine material carefully decanted and the dish reflooded. Separation of plant species was readily accomplished from the resulting suspension of stomach contents.

In the study of utilization of woody plants by deer on the Goldstream watershed, counts were made on 300 milacre-quadrats mechanically selected on each of the 3 major cover types, viz., new burn, second growth, and mature conifer forest. For each species the percentage of browsed plants was calculated and the severity of browsing recorded. Particular attention was given to the utilization of second growth Douglas fir.

To obtain a picture of the environment, to indicate seasonal availability, and to provide a basis for an enquiry into the selection of certain preferred forage species, a complete floral survey of the various plant communities on the two study areas was undertaken.

At intervals of varying length, dependent upon seasonal plant and deer activity, the study areas were examined, specimens of all newly appeared plant species collected, and notes made on the utilization of browse species by deer. Plants have been identified by Mrs. G. A. Hardy, botanist of the British Columbia Provincial Museum. In the case of certain difficult groups, specialists were consulted.

The mushrooms and lichens were exempted from the general survey. It was found so difficult to obtain reliable identifications of these plants that only those actually eaten by deer were dealt with.

No attempt was made to assess the occurrence of herbaceous species on a numerical basis. For the purpose of completeness this might have been desirable but the small importance of most of these plants from the standpoint of the deer did not justify the considerable expenditure of time that would have been involved.

Various numerical expressions of forage palatability have been used by workers on game and range surveys. The one most commonly used is that standardized by the United States Forest Service (1937). In this method palatability is expressed as "the per cent of the total current years growth, within reach of stock, to which a species is grazed when the range unit is properly utilized under the best practical range management." The recent designation of this concept as the "proper use factor" more nearly indicates its true nature than does "palatability." Stegman (1937) uses a slightly different rating based upon the "average percentage of the available portion of the species that have been browsed by deer." This author has derived his figures purely from summer observations and in consequence they are not comparable with those obtained from year-round studies.

These and all other similar attempts to give numerical palatability ratings examined have one fault

in common. From a personal estimate, which, depending upon the experience of the observer, partakes more or less of the qualities of a guess, quantitative results are derived and frequently expressed with a preciseness not warranted by the methods of derivation.

The experimental feeding conducted by Nichol (1938) probably represents the most satisfactory method yet applied of determining true palatability.

As has been found by other authors (Young & Robinette, 1939) there are many variables involved in the degree to which a forage species is used. Under low population pressure only the most desirable plants are extensively browsed, but as a game population increases through saturation to over-stocking progressively less desirable species will exhibit utilization approaching 100 per cent.

The degree to which any forage plant is utilized depends not alone upon the abundance of the browsing species, but equally upon the abundance of the browse species and upon the other components of the floral environment. For example a "palatability" rating for Douglas fir calculated under conditions obtaining in the second growth on the Goldstream area, where available individuals of this species average over 3,000 to the acre would be approximately 63 per cent. A similar calculation on the base of Mount Tzouhalem near Duncan, V. I., where the deer population is of about the same density but the fir incidence is only about 300 to the acre would be close to 100 per cent.

As has been shown by Mitchell & Hosley (1936) the same plant species under the same deer pressure may be browsed with significantly different intensity depending upon the concentration of certain chemical constituents in the soil upon which the plant is growing.

Palatability ratings are applicable only under the precise conditions obtaining when they were calculated. Their transfer by inference to other areas where different conditions prevail can lead to false conclusions, consequently they are of relatively minor importance except in local management studies. It has seemed to me much more important to attempt a segregation of the flora of the study areas into broad categories of highly palatable, moderately palatable, slightly palatable and unpalatable species as was done by Dixon (1934) in his study of the California Mule deer. Such findings are capable of broad application throughout the same floral province and provide the essential data for range reconnaissance.

It is a pleasure to acknowledge the co-operation I have received from Game Commissioners F. R. Butler and J. G. Cunningham of the British Columbia Game Commission and from Game Wardens R. S. Hayes of Duncan, B. C. and F. M. Wier of Cowichan Lake, B. C. P. W. Martin of Victoria, B. C., has accompanied me on much of the field work and has given valued aid as well during many of the more tedious phases of the investigation.

AREAS OF STUDY

The Goldstream Summit area comprises some thirty thousand acres on the watershed of the Goldstream River and includes several lakes and numerous ponds. (Map 2.) Butchart Lake, Lubbe Lake, Goldstream
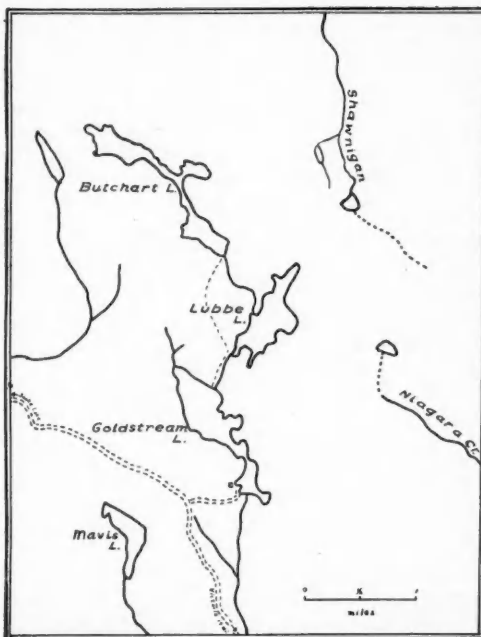
Map 2. Map of Goldstream Summit, Vancouver Island, B. C.

Lake, Mavis Lake and Jack Lake at an altitude of about fifteen hundred feet in rolling country are the source of Goldstream River. They vary in size from almost two miles long (Butchart Lake) to about three quarters of a mile long (Mavis Lake) and are all comparatively narrow, from two hundred yards to six hundred yards in width. Water from these lakes is used for hydro-electric and domestic purposes and to maintain a more uniform supply each of the lakes has its level artificially raised by damming. During dry summer the water level of Butchart, Lubbe and Goldstream lakes may fall as much as sixteen feet, with the consequent exposure of large areas of mud. Due to the sporadic nature of this exposure such mud flats are without vegetation. Mavis Lake on the other hand has regular summer low water about four to six feet below the spring level. Here the mudflats support an abundant and varied flora. Aquatic vegetation is virtually absent from all these lakes.

The Goldstream Summit area includes all the major biotic communities occurring at medium elevations on southern Vancouver Island. Approximately seventeen hundred acres were logged and burned in 1938 and are in the earliest stage of regeneration. Another three thousand acres were burned over in 1922. In places this burn destroyed all the original timber,

elsewhere about 25 per cent of the original stand is still present. The remainder of the area supports a semi-open subclimax forest of Douglas fir with the young growth mainly hemlock, cedar and balsam fir.

Hunting is prohibited on about 75 per cent of the Goldstream Summit but in actual practice the entire area is subjected to a fairly regular hunting drain.

Bald Mountain Game Reserve on the other hand is entirely protected and the enforcement is adequate to prevent all hunting. The reserve occupies a narrow-necked peninsula projecting into Cowichan Lake. It contains about twenty-two hundred acres of which eleven hundred acres have been logged. The remaining timber stands are mostly on the precipitous rocky slopes of Bald Mountain where the mature trees are Douglas fir with a small percentage of western hemlock. Near the top of the mountain, at two thousand feet, there are some jack pines *(Pinus contorta)* and a few junipers *(Juniperus scopulorum)*.

One block of four hundred and thirty-four acres logged and burned in 1915 and reburned in 1926 typifies the low elevation mesic burns of southern Vancouver Island (Fig. 1). A small portion of it escaped the 1926 burn and supports a fair stand of young firs. Elsewhere the new growth of woody plants is Arbutus, Spiraea, Salix, Alnus, Gaultheria, Cornus and Symphoricarpus together with some Pseudotsuga, Pinus, Tsuga and in the moist areas Thuja.

FIG. 1. Logged and burned area on Bald Mountain, Cowichan Lake, B. C.

MAJOR PLANT COMMUNITIES

In the Goldstream Summit and Bald Mountain study areas eight major plant communities available to deer were discernible. These are all stages in the seral succession leading to the coast forest climax Thuja-Tsuga formation of Clements (1928) though the mature forest on the areas has reached only the Douglas fir subclimax (Pseudotsuga consocies) stage.

At the time of examination these seral plant communities, divisible into dry ground series (Xerosere) and wet ground series (Hydrosere) were as follows:

Wet ground series: Hydrosere

Mud flat community: Rush-Sedge-Quillwort (Juncus-Carex-Isoetes) associes.

Sedge meadow community: Sedge-Water parsley (Carex-Oenanthe) associes.

Alder-willow community: Alder-Willow (Alnus-Salix) associes.

Dry ground series: Xerosere

Rock-bluff community: Moss-Hairgrass (Polytrichum-Aira) associes.

New burn community: Willowherb-Groundsel (Epilobium-Senecio) associes.

Coniferous pioneer forest community: Douglas fir-Salal (Pseudotsuga-Gaultheria) associes.

Deciduous pioneer forest community: Madrone-Spiraea-Salal (Arbutus-Spiraea-Gaultheria) associes.

Coniferous subclimax forest community: Douglas fir subclimax (Pseudotsuga consocies).

No attempt was made to subdivide these communities into their lesser components but each was surveyed intensively to determine its plant assemblage and the interaction between these and the deer.

WET GROUND SERIES

Mud flat community (Juncus-Carex-Isoetes associes)

This associes has very limited representation. I found it only on the shores of Mavis Lake, chiefly at its northern end (Fig. 2), but another small atypical example occurs on the shore of Lubbe Lake around the delta of Butchart Creek.

FIG. 2. Mud flat community, Mavis Lake, Goldstream Summit.

From October to June these flats are submerged beneath water varying from six inches to four feet in depth. From June until August the water level gradually recedes and herbaceous growth on the exposed ground becomes luxuriant. A high proportion of the species are peculiar to this community (Table 1).

The production of forage species palatable to deer is limited, but inasmuch as this herbage is succulent at a time when most of the surrounding terrain is undergoing severe desiccation there is a concentration of browsing effort here in July and August. The two dominant sedges *Carex oederi* and *C. kelloggii* provide the bulk of the browse. The rush *Juncus ensifolius* is eaten extensively but it is not abundant and consequently the browse value is small. *Juncus oreganus* the dominant, over large areas the only, plant species is not eaten at all. A large bed of quillwort *(Isoetes echinospora)* growing in the muddy

TABLE 1. Plants of the mud flat community at Goldstream Summit, and their utilization by deer.

Species	Period of availability	Period of utilization	Abundance	Importance as deer food
SHRUBS				
Spiraea douglasi	Apr.-Nov.	July-Sept.	scarce	low
Salix sitchensis	Apr.-Oct.	Apr.-Oct.	scarce	moderate
HERBACEOUS PLANTS				
Cardamine breweri	Apr.-May	Apr.-May	scarce	low
Lycopus uniflorus				
Mitella ovalis	Apr.-July	Apr.-May	scarce	low
Nymphaea polysepala	May-Sept.	not eaten	fair	none
Ranunculus bongardi	May-Sept.	not eaten	scarce	none
Ranunculus flammula	Apr.-Oct.	Apr.-July	abundant	moderate
Sanguisorba microcephalum	May-Aug.	not eaten	scarce	none
Trifolium repens	Apr.-Oct.	Apr.-Oct.	fair	moderate
GRASSES, SEDGES, RUSHES, ETC.				
Agrostis exarata	Apr.-Nov.	Apr.-May Oct.-Nov.	fair	moderate
Agrostis palustris	Apr.-Aug.	not eaten	fair	none
Alopecurus geniculatus	May-Aug.	May-July	fair	low
Bromus pacificus	Apr.-Oct.	Apr.-May	fair	low
Carex-kelloggii	June-Oct.	June-Sept.	abundant	high
Carex leersii	June-Oct.	June-July	fair	low
Carex oederi	May-Oct.	May-Sept.	abundant	high
Dulichium arundinaceum	June-Oct.	not eaten	fair	none
Eleocharis palustris	May-Oct.	not eaten	scarce	none
Equisetum arvensis	Apr.-Sept.	Apr.-May	fair	mod. to low
Isoetes echinospora	July-Nov.	Aug.-Nov.	fair	moderate
Juncus ensifolius	Apr.-Sept.	Apr.-June	fair	moderate
Juncus oreganus	June-Oct.	not eaten	abundant	none
Rhynchospora alba	June-Oct.	not eaten	fair	none
Sparganium simplex	June-Sept.	not eaten	scarce	none
Scirpus occidentalis	June-Sept.	not eaten	scarce	none
Typha latifolia	May-Sept.	not eaten	scarce	none

estuary of Butchart Creek was grazed to about 90 per cent when examined in October, 1938.

Sedge meadow community (Carex-Oenanthe associes)

In the Goldstream area this associes occupies about 3 per cent of the second growth forest land (Fig. 3).

FIG. 3. Sedge meadow community, Goldstream Summit. *Carex sitchensis* in foreground, Deschampsia behind.

Here it occurs in several different stages of development characterized by the local abundance of certain subdominant species.

The sedge meadows of the Bald Mountain area are successionally older and present several steps in the transition from the Carex-Oenanthe associes to the Alnus-Salix associes.

In general these meadows appear to have arisen by the gradual filling of shallow lakelets. They occupy the depressions between low hills, are perfectly flat, flood every spring to a depth of a foot or more and are usually drained by a small stream, the relic effluent of the pre-existing lakelet. Most of them are surrounded by a fringe of alders and willows, in others the firs, hemlocks, cedars and pines come down to the margin.

As the conifer forest develops many of the sedge meadow species perish from lack of light. For the same and other reasons cedar replaces the alder fringe and smaller sedge meadows gradually become cedar swamps. However, where the conifer forests are open the sedge meadow as a community has a long life.

While the sedges dominate the meadow flora many other species are present in abundance (Tables 2 and 3). In certain florally older meadows Myrica and *Spiraea douglasii* may be so abundant as to occupy the position of dominants.

TABLE 2. Plants of the sedge meadow community at Goldstream Summit, and their utilization by deer.

Species	Period of availability	Period of utilization	Abundance	Importance as deer food
TREES AND SHRUBS				
Kalmia polifolia	throughout year	not eaten	scarce	none
Ledum groenlandicum	" "	not eaten	scarce	none
Myrica gale	May-Oct.	June-Aug.	abundant	moderate
Salix sitchensis	Apr.-Nov.	Apr.-Nov.	scarce	low
Spiraea douglasii	May-Oct.	June-Sept.	fair	moderate
HERBACEOUS PLANTS				
Aster douglasii	May-Aug.	not eaten	scarce	none
Galium triflorum	Apr.-Sept.	Apr.-June	abundant	low
Gentiana sceptrum	June-Aug.	not eaten	abundant	none
Epilobium alpinum	May-Aug.	May-Aug.	scarce	low
Epilobium adenocaulon	May-Aug.	May-Aug.	abundant	moderate
Epilobium angustifolium	May-Aug.	May-Aug.	scarce	low
Hypericum bryophytum	May-Sept.	not eaten	very abund.	none
Hypericum scouleri	June-Sept.	not eaten	fair	none
Menyanthes trifoliata	May-Oct.	not eaten	scarce	none
Mimulus moschatus	Mar.-Nov.	Mar.-May	abundant	moderate
Nymphaea polysepala	May-Oct.	not eaten	scarce	none
Oenanthe sarmentosa	Apr.-Sept.	Apr.-Sept.	very abund.	high
Sanguisorba microcephalum	June-Aug.	not eaten	fair	none
Scutellaria galericulata	June-Oct.	not eaten	abundant	none
Trientalis arctica	May-July	not eaten	very abund.	none
Veronica scutellata	Apr.-Sept.	not eaten	abundant	none
Viola palustris	Apr.-Aug.	not eaten	fair	none
GRASSES, SEDGES, RUSHES, ETC.				
Agrostis hiemalis	Apr.-Aug.	not eaten	abundant	none
Botrychium sp.	July-Sept.	not eaten	scarce	none
Carex aquatilis	Mar.-Aug.	Mar.-May	abundant	low
Carex brunnescens	Apr.-Sept.	Apr.-Aug.	abundant	low
Carex interior	Mar.-Aug.	Mar.; July-Aug.	abundant	low
Carex siccata	Mar.-Aug.	not eaten	scarce	none
Carex sitchensis	Mar.-Aug.	Mar.-Apr. July-Aug.	very abundant	low
Carex stipata	Mar.-Aug.	not eaten	abundant	none
Deschampsia caespitosa	Apr.-July	not eaten	very abund.	none
Juncus ensifolius	Apr.-Sept.	Apr.-June	fair	moderate
Glyceria striata	Apr.-Nov.	Apr.-May Sept.-Nov.	abundant	moderate
Sparganium simplex	May-Nov.	not eaten	scarce	none

TABLE 3. Plants of the sedge meadow community at Bald Mountain, and their utilization by deer.

Species	Period of availability	Period of utilization	Abundance	Importance as deer food
TREES AND SHRUBS				
Salix sitchensis	Apr.-Oct.	Apr.-Oct.	abundant	high
Spiraea douglasii	May-Oct.	July-Sept.	abundant	moderate
HERBACEOUS PLANTS				
Galium triflorum	Apr.-Oct.	Apr.-May	abundant	low
Lysichiton kamschatkense	Apr.-Sept.	April	abundant	low
Mentha canadensis	May-Oct.	May-Oct.	abundant	moderate
Oenanthe sarmentosa	Apr.-Oct.	Apr.-Aug.	abundant	high
Veronica americana	Apr.-Oct.	not eaten	abundant	none
Viola palustris	Apr.-July	not eaten	scarce	none
Ranunculus aquatilis	June-Aug.	August	scarce	low
Ranunculus flammula	Mar.-Aug.	Apr.-June	fair	low
GRASSES, SEDGES, RUSHES, ETC.				
Agropyron pauciflorum	Mar.-Nov.	Mar.-May; Oct.-Nov.	fair	low
Cinna latifolia	Mar.-Nov.	Mar.-May	scarce	low
Carex oederi	Mar.-Oct.	Mar.-June	abundant	moderate
Carex retrosa	Mar.-Sept.	Mar.-Apr.	very abund.	low
Carex sitchensis	Mar.-Sept.	Mar.-Apr.	" "	low
Equisetum arvense	Apr.-Oct.	Apr.-Aug.	abundant	moderate
Struthiopteris spicant	throughout the year	Apr.-May; Dec.-Mar.	abundant	low
Typha latifolia	Apr.-Oct.	not eaten	abundant	none

During the spring and early summer deer spend much time in these meadows, but in spite of careful examination of the plants I have been able to discern little actual browsing. Myrica, Spiraea, Oenanthe, Juncus and the very young shoots of certain of the sedges are the only species I have found eaten appreciably and even these were but lightly utilized. Certain other species are nibbled occasionally. On the whole these sedge meadows are not an important source of food.

During July and August deer frequently bed down in the tall sedge. The evaporation from the moist ground serves to cool beds so located several degrees below the surrounding air temperature.

In the younger meadows, where water stays well on into midsummer, water parsley, *Oenanthe sarmentosa*, is the dominant plant, and sub dominants are *Glyceria striata, Veronica scutellata, Carex sitchensis, Equisetum arvense* and *Ranunculus flammula*. In such meadows Oenanthe is eaten heavily during the spring and summer, *Ranunculus flammula* is a favored spring browse and the Equisetum and Carex are eaten occasionally.

This associes in the Bald Mountain area is characterized by having less Oenanthe; *Veronica americana* replaces *V. scutellata; Carex rostrata* and *C. sitchensis* are dominants and *Mentha canadensis* is an important sub dominant along with *Equisetum arvense* and *Carex oederi*. (See Tables 2 and 3.)

Alder-willow community (Alnus-Salix associes)

This community is characteristic of the pioneer tree invasion upon moist habitats. A fringe of alders and willows surrounds most sedge meadows and lakes where suitable ground occurs. With maturity, and encroachment of the encircling conifer forest, the alder-willow associes gradually passes into the cedar-hemlock association.

TABLE 4. Plants of the alder community at Goldstream Summit, and their utilization by deer.

Species	Period of availability	Period of utilization	Abundance	Importance as deer food
TREES AND SHRUBS				
Alnus rubra	Apr.-Nov.	July-Nov.	abundant	moderate
Gaultheria shallon	throughout the year	throughout the year	abundant	high
Myrica gale	May-Sept.	July-Sept.	fair	low
Populus trichocarpa	Apr.-Oct.	Sept.-Oct.	scarce	low
Ribes lacustre	Apr.-Oct.	Apr.-Aug.	fair	low
Rubus macropetalus	Apr.-Dec.	Oct.-Dec.	fair	low
Rubus parviflorus	Apr.-Sept.	June-Aug.	fair	moderate
Rubus spectabilis	Apr.-Oct.	Apr.-July	fair	moderate
Rosa gymnocarpa	Apr.-Dec.	Apr.-Dec.	fair	low
Salix geyeriana	May-Oct.	Aug.-Oct.	fair	moderate
Salix lasiandra	May-Oct.	Aug.-Oct.	abundant	high
Salix sitchensis	May-Oct.	Aug.-Oct.	abundant	high
Salix scoulerians	May-Oct.	Aug.-Oct.	abundant	moderate
Sambucus racemosa	May-Sept.	May-June	scarce	low
Thuja plicata	throughout the year	Nov.-Mar.	scarce	low
Tsuga heterophylla	" "	none	fair	none
HERBACEOUS PLANTS				
Anaphilis margaritaceae	Apr.-Oct.	none	abundant	none
Boykinia occidentalis	June-Sept.	July-Aug.	scarce	low
Carduus arvense	Apr.-Sept.	Aug.-Oct.	fair	low
Cardamine breweri	Apr.-July	Apr.-May	scarce	low
Capsella bursa-pastoris	June-Aug.	July-Aug.	scarce	low
Epilobium adenocaulon	Apr.-Sept.	Apr.-July	abundant	moderate
Galium triflorum	Apr.-Sept.	Apr.-May	abundant	low
Gnaphalium palustre	Apr.-Sept.	none	fair	none
Gnaphalium purpureum	Apr.-Sept.	August	scarce	low
Lysichiton kamschatkense	Apr.-Sept.	April	scarce	low
Mimulus moschatus	Mar.-Oct.	Mar.-Apr.	abundant	low
Oenanthe sarmentosa	Apr.-Oct.	Apr.-Oct.	scarce	moderate
Ranunculus bongardi	Apr.-Sept.	none	scarce	none
Ranunculus flammula	Apr.-Sept.	Apr.-July	fair	moderate
Senecio sylvaticus	Apr.-Aug.	none	fair	none
Sonchus asper	May-Aug.	August	scarce	low
Stachys ciliata	Apr.-Sept.	Apr.-July	fair	low
Stellaria crispa	May-Oct.	July-Aug.	abundant	low
Tierella laciniata	May-Aug.	May-June	fair	low
Veronica scutellata	Mar.-Oct.	none	abundant	none
Veratrum viride	Apr.-Oct.	none	scarce	none
GRASSES, SEDGES AND RUSHES				
Agrostis palustris	Apr.-Oct.	none	very abund.	none
Agrostis exarata	Apr.-Oct.	Apr.-May	abundant	low
Bromus pacificus	Mar.-Dec.	Mar.-Apr.; Nov.-Dec.	abundant	moderate
Carex aquatilis	Mar.-Oct.	none	scarce	none
Carex interior	Mar.-Sept.	March	abundant	low
Carex oederi	Mar.-Sept.	Mar.-May	abundant	moderate
Carex siccata	Mar.-Sept.	none	scarce	none
Carex sitchensis	Mar.-Sept.	none	abundant	none
Carex stipata	Mar.-Sept.	none	abundant	none
Equisetum arvense	Apr.-Aug.	Apr.-May	abundant	moderate
Glyceria striata	Apr.-Dec.	Apr.-May; Nov.-Dec.	very abundant	moderate
Juncus acuminatus	Apr.-Sept.	Aug.-Sept.	fair	low
Juncus ensifolius	Apr.-Sept.	Apr.-May	fair	moderate
Luzula parviflora	Apr.-July	April	fair	low
Pteris aquilina	Apr.-Oct.	Apr.-Oct.	abundant	high

Where the alders and willows develop directly in the moist gullies of a new burn, growth is so rapid that few other plants can exist below the alder canopy and an alder consocies results. As a seral type following the maturity of the sedge meadow community the alder-willow associes develops slowly and intermediate stages exhibit considerable admixture of the sedge meadow plants.

TABLE 5. Plants of the alder community at Bald Mountain, and their utilization by deer.

Species	Period of availability	Period of utilization	Abundance	Importance as deer food
TREES AND SHRUBS				
Acer macrophyllum	May-Oct.	Sept.-Oct.	scarce	low
Alnus rubra	Apr.-Nov.	July-Nov.	very abund.	moderate
Cornus pubescens	Apr.-Oct.	Apr.-Oct.	scarce	low
Ribes sanguinea	Mar.-Oct.	Mar.-Oct.	fair	moderate
Rubus leucodermis	Apr.-Oct.	June-Oct.	scarce	moderate
Rubus macropetalus	Apr.-Oct.	July-Sept.	fair	low
Rubus parviflora	Apr.-Oct.	July-Sept.	fair	low
Rubus spectabilis	Apr.-Oct.	May-Oct.	abundant	moderate
Rosa nutkana	May-Feb.	Aug.-Feb.	scarce	low
Salix sitchensis	Apr.-Oct.	June-Oct.	abundant	moderate
Salix scouleriana	Apr.-Oct.	Sept.-Oct.	abundant	low
Symphoricarpos racemosa	Apr.-Jan.	Oct.-Jan	abundant	moderate
Thuja plicata	throughout the year	throughout the year	fair	moderate
HERBACEOUS PLANTS				
Adenocaulon bicolor	May-Sept.	July-Sept.	scarce	low
Achlys trifoliata	Apr.-Sept.	September	abundant	low
Capsella bursa-pastoris	May-Aug.	July-Aug.	scarce	low
Crepis biennis	June-Sept.	July-Aug.	fair	low
Crepis nicaensis	June-Sept.	July-Aug.	scarce	low
Erigeron canadensis	May-Aug.	not eaten	very scarce	none
Lysichiton kamschatkense	Apr.-Sept.	April	fair	low
Mentha canadensis	Apr.-Oct.	June-Aug.	fair	moderate
Oenanthe sarmentosa	Mar.-Sept.	Mar.-Sept.	fair	moderate
Petasites speciosus	Mar.-Sept.	Aug.-Sept.	scarce	low
Senecio triangularis	June-Sept.	not eaten	scarce	none
Stachys ciliata	Apr.-Sept.	May-July	scarce	low
Taraxacum officinale	Mar.-Sept.	Mar.-May	scarce	low
Tiarella trifoliata	Apr.-Sept.	July-Aug.	fair	low
Tolmiea menziesii	Apr.-Sept.	not eaten	scarce	none
Viola adunca	Apr.-Aug.	not eaten	fair	none
GRASSES, SEDGES, RUSHES, ETC.				
Adiantum pedatum	May-Sept.	August	scarce	low
Agropyron pauciflorum	Apr.-Nov.	Apr.-May	fair	low
Bromus vulgaris	Mar.-Dec.	Mar.-Apr.; Nov.-Dec.	abundant	moderate
Carex rostrata	Apr.-Sept.	not eaten	fair	none
Carex sitchensis	Apr.-Sept.	not eaten	fair	none
Cinna latifolia	Mar.-Dec.	Mar.-Apr.	fair	low
Equisetum hyemale	May-Aug.	July-Aug.	fair	low
Equisetum arvense	Apr.-Oct.	Apr.-May	abundant	low
Glyceria striata	Apr.-Dec.	Apr.-May	fair	moderate
Polystichum munitum	throughout the year	Jan.-Aug.	abundant	moderate
Pteris aquilina	Mar.-Oct.	Mar.-Oct.	very abund.	high
Struthiopteris spicant	throughout the year	July-Apr.	abundant	moderate

In dense stands of alder much of the forest floor is bare of herbaceous growth but in more open woodland with willows equalling alder in abundance of individuals a varied undergrowth develops. The alders and willows provide the bulk of the deer forage but such species as the deer fern *(Struthiopteris spicant)*, swamp gooseberry *(Ribes lacustre)*, sweet gale *(Myrica gale)* and others are eaten in small amounts. The plant assemblage in this community, its seasonal availability and its use by the deer are set forth in Tables 4 and 5.

DRY GROUND SERIES

Rock-bluff community (Polytrichum-Aira associes)

This community is not in the direct line of seral succession initiated as a result of logging and burning. The fire usually destroys the moss carpet on all rock areas and the residual earth is rapidly washed away by the heavy rains of the first succeeding winter. As a result a true primary pioneer associes often develops in such areas. However, inasmuch as earth does remain in the depressions and crevices the succession is more rapid than the original pioneer phase on the same site. Regeneration on the other denuded soil types is characterized by secondary pioneer flora and the seral communities follow one another rapidly. As a result the rock-bluff series frequently becomes modified by the shading effect imposed upon it by the more rapidly regenerating forest on adjacent areas.

The rock-bluff community, as used here, really includes small areas in various seral stages from crustose lichen to local grass and herb dominance (Fig. 4). From the standpoint of the deer these various

FIG. 4. Rock-bluff community, Goldstream Summit. Polytrichum and Aira dominant.

subdivisions are of little significance though the food potential increases from the moss stage through the grass and herb stages to reach a maximum when such trees and shrubs as salal, arbutus and spiraea assume dominance. With maturity of the surrounding conifer forest the rock-bluff series passes to a salal consocies thence apparently to a moss stage characterized by the shade-loving species, and by scattered plants of menziesia and other forest floor shrubs.

In the Goldstream Summit area the growing season in this community begins with the thaw in April and is complete by mid June. In July the bluffs become extremely arid and remain so until the autumnal rains begin in October. At that time certain of the grasses show some new growth and mushrooms become abundant.

The growing season at Bald Mountain begins roughly a month earlier and lasts somewhat longer than it does at Goldstream.

For the most part the flora of this community is not attractive to deer except for such shrubs and trees as Douglas fir, arbutus, salal and spiraea that extend in reduced numbers here from their surrounding centres of abundance. At Goldstream Summit two grasses *(Festuca rubra* and *Agropyron pauci-*

TABLE 6. Plants of the rock-bluff community at Goldstream Summit, and their utilization by deer.

Species	Period of availability	Period of utilization	Abundance	Importance as deer food
TREES AND SHRUBS				
Arctostaphylos uva-ursi	throughout the year	Jan.-Mar.	fair	low
Arbutus menziesii	"	Oct.-Mar.	scarce	low
Juniperus scopulorum	"	Jan.-Mar.	scarce	low
Cytisus scoparius	"	July-Aug.; Jan.-Mar.	scarce	low
Gaultheria shallon	"	throughout the year	abundant	high
Pseudotsuga taxifolia	"	"	abundant	high
Pinus contorta	"	none	fair	none
Rosa gymnocarpa	"	throughout the year	fair	low
HERBACEOUS PLANTS				
Achillea millefolium	May-Aug.	none	scarce	none
Agoseris heterophylla	Apr.-Aug.	none	scarce	none
Cardamine oligosperma	Mar.-May	Mar.-Apr.	abundant	low
Hieraceum albiflorum	Mar.-Sept.	July-Aug.	abundant	low
Hosackia parviflora	May-July	July	fair	low
Hypochaeris radicata	Apr.-Dec.	Apr.-June; Nov.-Dec.	abundant	moderate
Madia exigua	Apr.-June	none	abundant	none
Montia parvifolia	Apr.-June	none	abundant	none
Myosotis versicolor	Apr.-June	none	scarce	none
Sedum oreganum	throughout the year	Apr.-May	scarce	low
Senecio sylvaticus	Apr.-June	none	abundant	none
GRASSES, SEDGES, RUSHES, ETC.				
Agropyron pauciflorum	May-Dec.	May; Oct.-December	abundant	moderate
Agrostis hiemalis	May-Dec.	May	abundant	low
Aira praecox	Apr.-June	none	abundant	none
Festuca rubra	May-Dec.	May; Oct.-December	abundant	moderate
Morchella sp.	April	April	scarce	low

florum) and the cat's ear (Hypochaeris radicata) contribute moderately to the annual diet of the deer but other species (Table 6) are of little or no moment.

At Bald Mountain reserve (Table 7) the grass Elymus glaucus, a wild onion (Allium cernuum), and the spring beauty (Montia parviflora) are all preferred browse species. None of them is abundant enough to be of importance.

New burn community (Epilobium-Senecio associes)

In 1938 the burn on Goldstream Summit followed closely upon the completion of logging. It was largely a controlled burn and was comparatively harmless so far as actual destruction of deer was concerned. Virtually all green vegetation was eliminated but the roots of some perennial species survived.

This community occurred only upon the Goldstream Summit where the station selected for study lay to the north of and immediately adjoining the unlogged area surrounding Mavis Lake, and was the eastern limb of a burn extending westward and southward for a distance of about three miles (Fig. 5). Several small swamps and one lake were present on the burn, their sites marked by narrow fringes of cedar, hemlock and alder that had survived the fire.

As with the rock-bluff community the growth season is early and by mid August the dominant her-baceous annuals have matured their fruit and dried up.

Dominants in this associes are the dwarf fireweed (Epilobium minutum), and the groundsel (Senecio sylvaticus). There are local extensive socies in which

TABLE 7. Plants of the rock-bluff community at Bald Mountain, and their utilization by deer.

Species	Period of availability	Period of utilization	Abundance	Importance as deer food
TREES AND SHRUBS				
Arctostaphylus uva-ursi	throughout the year	Apr.; Jan.-March	scarce	low
Arbutus menziesii	"	Oct.-Mar.	abundant	high
Gaultheria shallon	"	throughout the year	abundant	high
Juniperus scopulorum	"	Jan.-Mar.	scarce	low
Pseudotsuga taxifolia	"	throughout the year	fair	high
Spiraea discolor	Apr.-Oct.	Apr.-Oct.	abundant	high
HERBACEOUS PLANTS				
Allium cernuum	Apr.-June	Apr.-June	abundant	moderate
Arabis hirsuta	Apr.-May	none	fair	none
Barbarea vulgaris	Mar.-May	none	very abund.	none
Camassia quamish	Mar.-June	Mar.-May	fair	moderate
Cardamine oligosperma	Mar.-Apr.	Mar.-Apr.	abundant	low
Fragaria chiloensis	Mar.-July	none	abundant	none
Gilia heterophylla	May-July	May-June	abundant	low
Heuchera micrantha	Apr.-July	Apr.-July	abundant	low
Hosackia parviflora	May-July	May-June	abundant	low
Mimulus langsdorfii	May-June	none	abundant	none
Mimulus alsinoides	Mar.-May	none	fair	none
Montia parviflora	Mar.-June	Mar.-June	fair	moderate
Montia parvifolia	Mar.-May	none	very abund.	none
Nemophila parviflora	Apr.-June	none	scarce	none
Saxifraga rufidula	Mar.-May	none	scarce	none
Valerianella congesta	Mar.-May	none	abundant	none
GRASSES, SEDGES, RUSHES, ETC.				
Aira caryophyllea	Apr.-June	none	abundant	none
Aira praecox	Mar.-May	Mar.-May	very abund.	low
Elymus glaucus	Apr.-July	Apr.-May	abundant	moderate
Festuca occidentalis	May-July	none	abundant	none
Festuca megalusa	Apr.-June	none	abundant	none
Lusula campestris	Mar.-May	Mar.-Apr.	abundant	low
Pellaea densa	throughout the year	Aug.-Mar.	scarce	low
Pityogramma triangularis	Feb.-Aug.	June-Aug.	scarce	low

FIG. 5. New burn community, Goldstream Summit, burned 1938, photographed 1944.

Lupinus latifolius is dominant. The flora of this area was characterized by the persistence of a number of the subclimax forest floor subdominants. Thus as will be seen in Table 13 salal, Oregon grape (*Berberis nervosa*), sword fern (*Polystichum munitum*), deer fern (*Struthiopteris spicant*) and hemlock are present in some numbers. In the early spring the salal and Oregon grape in particular made vigorous growth and appeared as community dominants, but the new growth soon withered and many plants failed to adapt themselves to the altered environment.

Table 8 lists the flora occurring in this community, the approximate numerical status of its constituents and their relative browse value to the coast deer. In Table 13 the woody plants are dealt with in more detail.

As already indicated the flora of the community consists of certain relic species present in the sub-

TABLE 8. Plants of the new burn community at Goldstream Summit, and their utilization by deer.

Species	Period of availability	Period of utilization	Abundance	Importance as deer food
TREES AND SHRUBS				
Abies grandis	throughout the year	Dec.-May	scarce	low
Arbutus menziesii	"	Oct.-Mar.	very scarce	low
Berberis nervosa	"	Jan.-May	abundant	moderate
Gaultheria shallon	"	throughout the year	very abund.	high
Pseudotsuga taxifolia	"	"	fair	moderate
Ribes lacustre	Apr.-Sept.	Apr.-Sept.	scarce	low
Rosa gymnocarpa	throughout the year	throughout the year	fair	low
Rubus macropetalus	"	June-July; Dec.-Mar.	fair	moderate
Rubus leucodermis	Apr.-Oct.	June-Oct.	fair	moderate
Thuja plicata	throughout the year	throughout the year	fair	moderate
Tsuga heterophylla	"	none	abundant	none
HERBACEOUS PLANTS				
Achlys triphylla	Apr.-July	none	abundant	none
Agoseris laciniata	Apr.-Dec.	Apr.-Dec.	scarce	low
Antennaria eximia	May-July	none	fair	none
Carduus edulis	Mar.-July	Mar.-Apr.	fair	low
Carduus lanceolatus	Apr.-July	none	fair	none
Epilobium adenocaulon	Apr.-Aug.	May-July	fair	moderate
Epilobium minutum	Apr.-Aug.	May-Aug.	very abund.	low
Galium biflorum	Apr.-Aug.	April	abundant	low
Hieraceum albiflorum	Mar.-Aug.	July-Aug.	abundant	low
Hypochaeris radicata	Apr.-Dec.	Apr.-Dec.	abundant	moderate
Lactuca muralis	Apr.-July	May-July	fair	low
Linnaea borealis	throughout the year	none	fair	none
Lupinus latifolius	May-July	June	very abund.	low
Mitella pentandra	Apr.-July	April	fair	low
Rumex acetosella	May-Aug.	none	abundant	none
Senecio sylvaticus	Apr.-July	none	very abund.	none
Sonchus asper	May-July	July	scarce	low
Viola sempervirens	throughout the year	none	fair	none
GRASSES, SEDGES, RUSHES, ETC.				
Anthoxanthum odoratum	throughout the year	Nov.-May	abundant	moderate
Asplenium felix-foemina	Apr.-July	none	scarce	none
Bromus vulgaris	Nov.-Aug.	Nov.-May	fair	moderate
Festuca occidentalis	Apr.-Aug.	April	abundant	moderate
Polystichum munitum	throughout the year	July; Jan.-March	abundant	moderate
Pteris aquilina	May-Oct.	May-Oct.	fair	moderate

climax forest community before logging, together with an abundant and varied assemblage of annual and perennial pioneers. Many of the latter are individually abundant but all are of little or no palatability and contribute little to the deer carrying capacity of the community. In this group are groundsel, cat's ear, dwarf fireweed, sorrel, lupine and most of the grasses. These are quick growing species that appear early and mature their seed by mid July or early August. Consequently mid-summer finds the available deer food limited to the winter browse species, of which salal and sword fern are the most noteworthy, to a few grasses, and to the rather sparse population of black raspberry (*Ribes leucodermis*) and other palatable shrubs.

The deer carrying capacity of the community is extremely low. Lack of cover renders it unattractive in mid-summer and in the cold winter weather. During winter and spring the salal, berberis and sword fern are subjected to intensive browsing and in early spring certain of the grasses are moderately utilized. It is significant that not one of the dominants or major subdominants contributes appreciably to the deer food supply. Less than 1 per cent of the lupines show any sign of browsing, only about 5 per cent of the fireweed plants are browsed and the groundsel is avoided completely.

Coniferous pioneer forest community (*Pseudotsuga-Gaultheria associes*)

This is one of the most extensive habitat types on southern Vancouver Island, and together with the next it provides the most important deer habitat in coastal British Columbia.

In the Goldstream Summit area the station chosen for intensive study had a thin stand of mature trees present on certain of the ridges (Fig. 6). The trunks

FIG. 6. Coniferous pioneer forest community, Goldstream Summit. Pseudotsuga, *Pinus contorta* and *Pinus monticola*. Several Pseudotsuga show severe deer damage. Deforested 1922, photographed 1944.

and branches of these provided an abundant supply of the important food lichen *Usnea barbata* as well as of other less important palatable arboreal lichens. They thus contribute significantly to the food potential of the community.

TABLE 9. Plants of the coniferous pioneer forest community at Goldstream Summit, and their utilization by deer.

Species	Period of availability	Period of utilization	Abundance	Importance as deer food
TREES AND SHRUBS				
Alnus rubra	Apr.-Nov.	May-Nov.	fair	low
Arbutus menziesii	throughout the year	Nov.-Mar.	very scarce	low
Arctostaphylos columbiana	"	Dec.-Mar.	scarce	low
Arctostaphylos uva-ursi	"	Dec.-Mar.	fair	low
Berberis aquifolium	"	Apr.-May; Jan.-Mar.	scarce	low
Berberis nervosa	"	Apr.-June; Dec.-Mar.	abundant	moderate
Gaultheria shallon	"	throughout the year	very abund.	high
Pinus contorta	"	none	fair	none
Pinus monticola	"	none	scarce	none
Pseudotsuga taxifolia	"	throughout the year	very abund.	high
Ribes lobbii	Apr.-Oct.	Apr.;July-August	fair	low
Ribes sanguinea	Apr.-Oct.	Apr.-Oct.	very scarce	low
Rosa gymnocarpa	throughout the year	throughout the year	fair	moderate
Rubus leucodermis	Apr.-Oct.	Apr.-Oct.	scarce	low
Rubus macropetalus	throughout the year	Dec.-Mar.	fair	low
Salix scouleriana	Apr.-Nov.	Apr.-Nov.	abundant	moderate
Salix sitchensis	Apr.-Nov.	Apr.-Nov.	abundant	moderate
Spiraea discolor	Apr.-Oct.	Apr.-Aug.	very scarce	low
Thuja plicata	throughout the year	Oct.-Mar.	fair	low
Tsuga heterophylla	"	not eaten	very scarce	none
Vaccinium ovatum	"	not eaten	very scarce	none
Vaccinium parvifolium	Apr.-Oct.	Apr.-Oct.	abundant	moderate
HERBACEOUS PLANTS				
Achillea millefolium	Apr.-Aug.	not eaten	fair	none
Adenocaulon bicolor	May-Aug.	June-July	scarce	low
Antennaria eximia	May-July	not eaten	fair	none
Carduus edulis	Mar.-Aug.	Mar.-Apr.	fair	low
Dicentra formosa	Apr.-Oct.	not eaten	very scarce	none
Gnaphalium microcephalum	Apr.-Aug.	not eaten	scarce	none
Hieracium albiflorum	Feb.-Sept.	July-Aug.	abundant	low
Hypochaeris radicata	throughout the year	throughout the year	abundant	moderate
Lactuca muralis	Apr.-Aug.	July-Aug.	fair	low
Linnaea borealis	throughout the year	not eaten	fair	none
Lupinus latifolius	June-Aug.	July	fair	low
Micromeria douglasii	throughout the year	not eaten	scarce	none
Senecio sylvaticus	Apr.-July	not eaten	scarce	none
Taraxacum officinale	Apr.-July	Apr.-May	scarce	low
Trifolium agrarium	May-Aug.	not eaten	fair	none
Viola sempervirens	throughout the year	Mar.-Apr.	fair	low
GRASSES, SEDGES, RUSHES, ETC.				
Agrostis exarata	Apr.-Nov.	not eaten	fair	none
Agrostis stolonifera	Apr.-Aug.	not eaten	fair	none
Anthoxanthum odoratum	Apr.-Jan.	Apr.-May; Dec.-Jan.	abundant	moderate
Bromus carcinatus	Apr.-Nov.	Apr.-May	fair	low
Boletus sp.	Nov.-Jan.	Nov.-Jan.	fair	moderate
Clitocybe gigantea	Nov.-Dec.	Nov.-Dec.	scarce	low
Cystopteris fragilis	throughout the year	not eaten	scarce	none
Elymus glaucus	Apr.-Oct.	Apr.-May	fair	low
Juncus tenuis	Apr.-July	not eaten	very scarce	none
Lycopodium annotinum	throughout the year	Feb.-Mar.	scarce	low
Poa pratensis	Apr.-Aug.	April	fair	low
Polystichum lonchitis	throughout the year	not eaten	scarce	none
Russula atropurpurea	Nov.-Dec.	Nov.-Dec.	scarce	low
Struthiopteris spicant	throughout the year	Apr.-May; Jan.-Mar.	fair	low
Usnea barbata	"	Nov.-Mar.	abundant	high

Both here and on the Bald Mountain area Douglas fir, salal and bracken (Pteris aquilina) are dominants. Data regarding the complete plant assemblage is given in Table 9.

In this community, unlike the recent burn, the abundant plant species are at the same time highly palatable to the deer and therefore represent a very high concentration of palatable browse. As is shown by the stomach content study conducted on the Goldstream area the major part of the annual food supply is provided by the Douglas fir, Usnea, salal, willow and alder. All of these are present as dominants or abundant subdominants. Besides providing abundant food the second growth fir community possesses ample cover for summer and winter bedding grounds.

Deciduous pioneer forest community (Arbutus-Spiraea-Gaultheria associes)

The Arbutus-Spiraea community is absent from the Goldstream area from which it is debarred by altitude (Fig. 7). On the Bald Mountain peninsula

FIG. 7. Deciduous pioneer forest community, Goldstream Summit, Alnus rubra and Salix sitchensis dominant. Deforested 1938, photographed 1944.

it is characteristic of regeneration on the southern slopes. Elsewhere on southeastern Vancouver Island it is widespread at low elevations.

Dominants in the Bald Mountain area are salal, arbutus and the tree spiraea (Spiraea discolor), important sub dominants are cat's ear (Hypochaeris radicata), snowberry (Symphoricarpos racemosa) and willow.

As a community this one is rich in palatable browse species. The three dominants and the three important subdominants already mentioned are all among the most sought after forage plants on Vancouver Island. The associes is also rich in secondary species of high palatability such as flowering currant (Ribes sanguinea), broad-leaf and smooth maple (Acer macrophyllum and A. glabra), flowering dogwood (Cornus nuttallii) and many others of lesser importance. These all assist in building up the carrying capacity of this habitat type.

The above species are favorably divided as to seasonal availability so that a year-round food supply is provided. Data as to availability and complete list of all plants collected in this community are given in Table 10.

TABLE 10. Plants of the deciduous pioneer community at Bald Mountain, and their utilization by deer.

Species	Period of availability	Period of utilization	Abundance	Importance as deer food
TREES AND SHRUBS				
Acer glabra	May-Oct.	May; Oct.	scarce	low
Acer macrophyllum	May-Oct.	May-June; Sept.-Oct.	fair	low
Alnus rubra	Apr.-Oct.	Apr.-Oct.	abundant	moderate
Arbutus menziesii	throughout the year	Oct.-Mar.	very abund.	high
Arctostaphylos tomentosa	"	Mar.-Apr.	scarce	low
Berberis aquifolium	"	Dec.-July	scarce	low
Berberis nervosa	"	Dec.-July	abundant	moderate
Cornus nuttallii	Apr.-Oct.	Apr.-Oct.	fair	moderate
Gaultheria shallon	throughout the year	throughout the year	very abundant	high
Pinus monticola	"	Jan.-Mar.	scarce	low
Pseudotsuga taxifolia	"	throughout the year	abundant	high
Ribes lobbii	Apr.-Oct.	Apr.-May; August	fair	low
Ribes sanguinea	Apr.-Oct.	Apr.-Oct.	fair	moderate
Rosa gymnocarpa	thoughout the year	throughout the year	abundant	moderate
Rubus leucodermis	May-Oct.	July-Oct.	scarce	low
Rubus macropetalus	throughout the year	Nov.-Mar.	abundant	low
Salix scouleriana	Apr.-Oct.	Apr.-Oct.	abundant	high
Salix sitchensis	Apr.-Oct.	Apr.-Oct.	abundant	high
Spiraea discolor	Apr.-Nov.	Apr.-Nov.	very abund.	high
Symphoricarpos racemosa	May-Jan.	May-Jan.	very abund.	high
Taxus brevifolia	throughout the year	Dec.-May	scarce	low
Thuja plicata	"	Dec.-Mar.	fair	moderate
Tsuga heterophylla	"	none	fair	none
Vaccinium parvifolium	Apr.-Oct.	Apr.-Oct.	fair	moderate
HERBACEOUS PLANTS				
Achillea millefolium	Mar.-Aug.	none	very abund.	none
Adenocaulon bicolor	Apr.-Sept.	July-Aug.	scarce	low
Carduus edulis	Jan.-July	Jan.-Mar.	fair	low
Cerastium arvense	Mar.-Nov.	Mar.-Nov.	abundant	moderate
Cerastium viscosum	Mar.-July	April	abundant	low
Crepis biennis	June-Sept.	July-Aug.	scarce	low
Epilobium angustifolium	Apr.-Sept.	May-July	scarce	low
Erigeron canadensis	May-Aug.	none	scarce	none
Galium aparine	Mar.-July	April	abundant	low
Hieraceum albiflorum	Feb.-Oct.	July-Aug.	abundant	low
Hypochaeris radicata	throughout the year	throughout the year	very abundant	high
Linnaea borealis	"	none	fair	none
Luina hyperleuca	June-Oct.	none	scarce	none
Lupinus latifolius	May-Aug.	July	abundant	low
Montia sibirica	Mar.-June	none	scarce	none
Micromeria douglasii	throughout the year	none	fair	none
Senecio fastigiatus	Mar.-Aug.	none	fair	none
Senecio triangularis	May-Sept.	none	scarce	none
Taraxacum officinale	Mar.-July	Mar.-May	fair	low
Tiarella laciniata	Mar.-Nov.	Mar.-May	fair	low
Tolmiea menziesii	Apr.-Sept.	none	scarce	none
Viccia sativa	Apr.-July	May	scarce	low
Viola adunca	Apr.-July	none	fair	none
Viola sempervirens	throughout the year	none	abundant	none
GRASSES, SEDGES, RUSHES, ETC.				
Adiantum pedatum	Apr.-Oct.	July-Aug.	fair	low
Anthoxanthum odoratum	throughout the year	Jan.-May	abundant	moderate
Athyrium felix-foemina	Apr.-Sept.	May	scarce	low
Bromus vulgaris	throughout the year	Dec.-May	abundant	moderate
Equisetum arvense	Apr.-Sept.	Apr.-May	abundant	moderate
Lycopodium annotinum	throughout the year	Jan.-Mar.	scarce	low
Luzula campestris	Mar.-June	Mar.-Apr.	abundant	low
Pteris aquilina	Apr.-Oct.	Apr.-Oct.	very abund.	high

Coniferous subclimax forest community (Pseudotsuga consocies)

The mature Douglas fir forest in process of transition to the climax hemlock-balsam-cedar forest is poor in variety of species. Over vast areas salal and sword fern are the characteristic ground cover in a landscape dominated by the boles of the giant conifers (Fig. 8). Under certain conditions various

FIG. 8. Coniferous subclimax forest community, Goldstream Summit. Pseudotsuga consocies, young trees are Tsuga, undergrowth is Polystichum and Gaultheria.

huckleberries or blueberries (*Vaccinium parvifolium* Smith, *V. ovatum* Pursh and *V. ovalifolium* Smith) replace the salal.

The flora of the section of forest on Goldstream Summit chosen for study is enriched by the inclusion in it of a lake shore. Along the exposed shore certain large firs blown down during gales have provided fresh soil that has been promptly occupied by some species characteristic of the more open communities.

At Goldstream Summit subdominants beneath the forest ceiling are hemlock and salal. In Table 11 is given the entire plant assemblage of this cover type and the seasonal availability of the components. In Table 14 the woody plants are considered in more detail.

Of the preferred browse species only salal is abundant in this community and it together with the Usnea supplies the bulk of the deer food.

The Goldstream example of the subclimax conifer forest is typical of the Usnea producing forests. Though I have been unable to determine what the limiting environmental conditions are, this lichen is absent from the west coast conifer forest and many of the more dense stands elsewhere on Vancouver Island and the adjoining mainland. It thrives on the limbs and boles of Douglas firs growing in the less humid (annual precipitation up to about 60 inches) parts of the British Columbia coast where the firs form open stands and do not normally attain heights in excess of 50-75 feet.

The deer carrying capacity of this community is on the average less than half that of the second growth fir community. But where it adjoins the latter it is often used as sheltered bedding ground.

TABLE 11. Plants of the Douglas fir subclimax community at Goldstream Summit, and their utilization by deer.

Species	Period of availability	Period of utilization	Abundance	Importance as deer food
TREES AND SHRUBS				
Abies grandis	throughout the year	Apr.-June	scarce	low
Berberis nervosa	"	Dec.-Mar.	abundant	moderate
Gaultheria shallon	"	throughout the year	very abundant	moderate
Pinus monticola	"	none	scarce	none
Pseudotsuga taxifolia	"	Apr.-June; Jan.-Mar.	scarce	low
Ribes lacustre	Apr.-Sept.	Apr.-Aug.	scarce	low
Ribes lobbii	Apr.-Sept.	July-Aug.	scarce	low
Rubus spectabilis	Apr.-Sept.	Apr.-Sept.	scarce	low
Rubus macropetalus	throughout the year	Aug.-Mar.	fair	moderate
Thuja plicata	"	throughout the year	fair	moderate
Tsuga heterophylla	"	none	fair	none
Vaccinium parvifolium	Apr.-Sept.	Apr.-Sept.	fair	moderate
HERBACEOUS PLANTS				
Achillea millefolium	May-Aug.	none	scarce	none
Achlys trifolium	Apr.-July	none	abundant	none
Chimaphila umbellata	throughout the year	Feb.-Mar.	fair	low
Dicentra formosa	Apr.-Sept.	none	scarce	none
Lactuca muralis	Apr.-July	Apr.-July	scarce	low
Mitella ovalis	Apr.-Aug.	May-June	fair	low
Montia sibirica	May-July	none	scarce	none
Pyrola picta	June-July	June	scarce	low
Sonchus asper	June-Aug.	June-July	very scarce	low
Tiarella laciniata	May-Aug.	May-Aug.	abundant	low
Trientalis sp.	Apr.-June	none	abundant	none
GRASSES, FERNS, ETC.				
Boletus sp.	Sept.-Jan.	Sept.-Jan.	abundant	moderate
Lusula parviflora	Apr.-June	April	abundant	low
Polypodium sp.	throughout the year	none	scarce	none
Polystichum lonchitis	"	April	scarce	low
Polystichum munitum	"	Apr.-June; Dec.-Mar.	abundant	moderate
Pteris aquilina	Apr.-Oct.	Apr.-Oct.	abundant	moderate
Usnea barbata	Nov.-Mar.	Nov.-Mar.	abundant	high

FEEDING HABITS OF THE COAST DEER

A number of peculiarities in the feeding habits of the coast deer have been noted. Many of these exert a directive influence upon the nature of the environment as it is affected by deer.

When the deer is grazing upon grass or other low growing herbaceous vegetation there is no dissimilarity with other grazing artiodactyls. The vegetation is broken off with either an upward, or less frequently, a downward motion of the head while grasped between the lower incisors and the premaxillary pad.

Browsing upon soft deciduous vegetation is sometimes accomplished similarly, for instance, leaves of alder, willow, maple, spiraea and dogwood are often plucked and eaten thus. When browsing hard vegetation, such as salal, or when feeding on twigs of any woody plants the severing is accomplished with the cheek teeth.

There is a strong preference for feeding with the front feet higher than the back that leads to heavier utilization of the downhill side of shrubs growing on steep hillsides. Possibly this tendency together with a marked proclivity for feeding where the eyes as well as the ears and nose can be used to advantage leads to a heavier utilization of browse growing on hills than on adjoining flat areas.

Certain species of grass are grazed heavily in the spring and sporadically in the summer and autumn. I have noticed a strong aversion to grass seed. This was particularly obvious on the shores of Goldstream Lake in October 1939. The summer had been very dry and grass in consequence more heavily grazed than usual. Many grass clumps had all the blades eaten down but seed heads were untouched. Personal observations of semi-tame deer confirm this habit. The importance of this habit upon the survival and spread of the grasses is obvious. At the same time the avoidance of grass seed probably serves to protect the deer from the dangerous mouth lesions caused by the sharp glumes of certain bromes and fox tails.

A feeding deer undisturbed by flies moves slowly forward browsing a few mouthfuls off one shrub a few from another with frequent pauses to look and listen. At Cowichan Lake on August 26, 1939, I timed several does and fawns and found them to move on the average about 100 yards in 25 minutes feeding. Later the same day a small doe harried by Tabanids was observed feeding on berries in a large salal bottom. She moved at a fast walk, occasionally breaking into a trot and covered approximately half a mile in half an hour.

The coast deer evinces considerable selection in its feeding. As is set forth in the section on food species, certain plants are avoided while others are assiduously sought for, and every specimen browsed. On the Goldstream Lake area *Vaccinium parvifolium* was in the latter category, while on the Cowichan Lake area *V. parvifolium* and *Ribes sanguinea* were the two species most notable in this regard. During the winter months *Usnea barbata* occupies an important place in the diet out of all proportion to its availability, evidence of its preferred food status.

However, even where such preferred food species are sufficiently abundant to provide, temporarily at least, the entire bulk of food needed by the deer stock, I have observed no instance of a deer making as much as one entire meal of a single plant species.

I was struck with the ability of the coast deer to distinguish between a good acorn and a hollow one. I repeatedly offered mixtures of both to the captive deer in Beaconhill Park, Victoria. Apparently the deer could differentiate them by smell from a distance of about three inches, not once did it take a hollow one into its mouth. The acorns of *Quercus garryana* were shelled before being eaten and the shells extruded from the sides of the mouth.

Certain of the preferred mushrooms, such as *Clitocybe gigantea* are dug from the ground and eaten as soon as they begin to break the soil. At Comox on October 13, 1931, I examined many places where this had been done. Though I have not personally witnessed a deer digging up a mushroom, the evidence of tracks left at the spot indicates that it is

done with the fore hoofs. These are apparently stamped into the ground and the underlying mushroom "kicked" out.

The coast deer avoids swamps where the water reaches above its knees, or where there is deep soft mud. In no instance has browsing on even preferred food species been observed where wading in deep water would have been involved. Only infrequently have I noted browsing on leaves beneath the water surface. In April, 1940 on the Goldstream Summit I found two ponds in which the *Ranunculus flammula* and the Oenanthe had been browsed to about 3 inches below the water surface, but this was the only instance noted in 10 years observation.

It has long been recognized that more than mere availability is involved in the utilization of a certain browse species by deer. There are species of high palatability and species of little or no palatability. Apart from this distinction between the attractiveness as food of a given plant I have observed certain psychological characteristics that influence the feeding habits of the deer.

It has been repeatedly observed that the coast deer dislikes to force its way into a thicket to feed. It prefers to feed in the open. Consequently plants of a given species growing around the margins of clearings or in open stands are heavily browsed while those in the centers of thickets may be untouched. This habit in the long run tends to maintain the clearings and open stands and thereby to retard the transition to the subclimax or climax forests of low food potential. A further consideration of this habit is given in the section on utilization of Douglas fir.

It was repeatedly observed that thorns had a very real protective value to the plant possessor. For example, the comparatively unarmed thistle *Carduus edulis* is eaten extensively when young while the heavily spined *Carduus lanceolatus* is avoided. Similarly the soft spined *Ribes lacustre* is browsed more extensively than the long spined *R. lobbii*. The fruits of both these gooseberries are eaten only on the outside of the bushes, those in the centre of the bushes where they are protected by the thorns are seldom touched. The roses though of high palatability are usually subjected only to leaf browsing which is much less damaging to the plant than removal of the entire terminal twig. It is of course possible that palatability apart from the presence and absence of thorns is operative in the case of the thistles and the gooseberries but observation of the deer feeding upon these species leads me to the conclusion that the spines are the main deterrent.

TREES AND SHRUBS OF THE GOLDSTREAM SECOND GROWTH FIR AREA AND THEIR UTILIZATION BY DEER

Food habit studies of the extensive type conducted in the Goldstream area soon revealed that the second growth fir area was by far the most important one both from the standpoint of total number of deer feeding in this area and from the length of the seasonal use of its shrub and tree species.

It was obvious also that the degree of utilization to which the second growth Pseudotsuga was subjected assumed serious proportions.

In view of these considerations it was deemed worth while to make a more intensive study of the floral composition of this cover type and the extent of its utilization.

By repeated censuses it was determined that the population of deer in this cover type averaged in the vicinity of 30-35 deer per square mile. Censuses were taken periodically in all seasons over a period of three years and the population found to be relatively stable.

For the purpose of the study a representative area of approximately 640 acres was chosen on the west side of Goldstream Lake. By random sampling 300 milacre quadrats were selected. On each of these a tabulation was made of the number of individual plants present and the extent to which such plants had been browsed by deer.

In the case of all species except the salal *(Gaultheria shallon)* rooted stems were used as criterion in determining number of individual plants. Each rooted stem was listed as a separate plant. It was not found practicable to do this for salal and in this species notes were made of the presence of the plant and the proportion of the soil surface covered by it.

It was found that two types of Douglas fir were present on the area. These were readily distinguishable by colour and by form of the needles. Approximately four-fifths of the trees were normal in form, the needles long, characteristically lax and of a dark green colour. The other fifth of the trees had the needles appreciably shorter, stiffer and yellow-green in colour. This difference was thought to result from environmental factors but no satisfactory explanation was developed. The distinction was not observed in trees more than seven to ten feet in height. It may be significant to note that in 17 instances both green and yellow trees were present on the same milacre quadrat. This tends to eliminate from consideration environmental factors of such general application as soil moisture. No difference in the mortality rate of the two types was observed.

Because even a casual examination made it plain that the light green or yellow trees were but slightly browsed while the dark green trees were heavily utilized the two types were censused separately. The results are considered in more detail below.

To facilitate comparison the census figures have been reduced to trees per acre. Table 12 presents this data together with the percentage of plants showing browsing.

For the purpose of this census the area was not subdivided into its component communities. The quadrats were located at random in all the plant communities occurring in this second growth fir cover type. While the numbers are small and in consequence their reliability limited it was found that in the 640 acres studied, of every one thousand quadrats (one acre) thirty quadrats were located in the alder community. Twenty-three quadrats were in sedge meadow, one hundred and seven in open rock bluffs and the remainder comprised the second growth

TABLE 12. Trees and shrubs per acre on Goldstream second growth fir area and their utilization as deer food. Data derived from 300 milacre quadrats reduced to a 1000 quadrat (1 acre) basis.

Species	Total number of plants	Number of quadrats on which species occurred	Per cent heavily browsed	Per cent lightly browsed	Total browsing per cent
Pseudotsuga taxifolia (green)	3567	673	56%	7%	63%
Pseudotsuga taxifolia (yellow)	800	93	3%	3%	6%
Vaccinium parvifolium	117	77	100%	....	100%
Thuja plicata	107	40	80%	7%	87%
Tsuga heterophylla	40	27	....	....	0
Pinus monticola	13	13	....	....	0
Arctostaphylos uva-ursi	17	13	25%	50%	75%
Myrica gale	10	3	....	50%	50%*
Salix sp.	10	3	10%	70%	80%*
Arctostaphylos columbianum	7	7	....	50%	50%*
Ribes lacustre	7	3	....	30%	30%*
Ribes lobbii	2	2	....	10%	10%*
Chimaphila umbellata	50	17	....	4%	4%*
Rosa gymnocarpa	10	10	....	90%	90%
Pinus contorta	4	4	....	....	0
Gaultheria shallon	..	900	....	....	32%
Berberis nervosa	511	137	....	30%	30%
Alnus rubra	†150	50			

*Utilization based upon counts in which each species is represented at least 50 times.
†Alder twigs seldom browsed, only the leaf is eaten, therefore this census gives no reliable data on utilization. 90 per cent of trees over 7 feet.

fir community in its specific sense as used elsewhere in the paper.

If we assume then that these figures provide a reliable indicator of the percentage composition of plant communities included in the 1922 burn on Goldstream Summit we find that 84 per cent is land upon which a second growth fir forest is developing, 10.7 per cent is exposed rock with or without moss carpet, 3 per cent is hygric salal-alder or salal-cedar bottomland (alder community and developing coniferous climax community) and 2.3 per cent is sedge meadow.

As already stated my census figures are based on the entire area not just upon the 84 per cent supporting second growth fir.

Trees included in the table were of height classes from three inches to six feet. In addition to trees of these classes the area also supported on each acre an average of thirty-seven mature Douglas fir trees and another sixty-three between seven feet and twenty feet in height. Other species present but not included in the table are *Arbutus menziesii* about one plant to one hundred acres, *Vaccinium ovatum* about one plant to one thousand acres and *Spiraea discolor* about one plant to five hundred acres.

The census was conducted during the first week in April, 1940, as it was ascertained that at that time the shrubby plants had suffered about the maximum utilization of the new growth of the previous year. It will be obvious that all herbaceous species are excluded from this inventory.

If it was deemed from inspection that 50 per cent or more of the annual growth had been removed or if, in the case of Douglas fir the leader had been removed, the browsing was recorded as serious. Otherwise it was recorded as light or non-existent as the case might be

From Table 12 it will be seen that the Douglas fir is numerically the most important species. A total of 4,367 individual fir trees under six feet in height was the average density per acre at the time the census was conducted. Of these 3,567 were "green" and 800 "yellow." Sixty-three per cent of the green trees were browsed, 56 per cent seriously, 7 per cent lightly, whereas only 6 per cent of the yellow trees showed browsing and only 3 per cent had been topped.

The most sought-after shrub on the area was the red huckleberry (*Vaccinium parvifolium*) which though widely distributed and not numerically abundant had been hunted out and every bush browsed. The extent of this utilization was severe, from 90 per cent to 100 per cent of the annual growth being removed (Fig. 4). The effect on the plants is to reduce them to dense "brushes" and to practically eliminate the production of fruit.

Utilization of the giant cedar was similarly severe. Eighty-seven per cent of the trees had been browsed, 80 per cent severely. In most instances the young cedars had been unable to reach a height of more than a foot or two and repeated cropping had resulted in the production of spiny juniper-like needles in place of the normal soft scale-like leaf (Fig. 9).
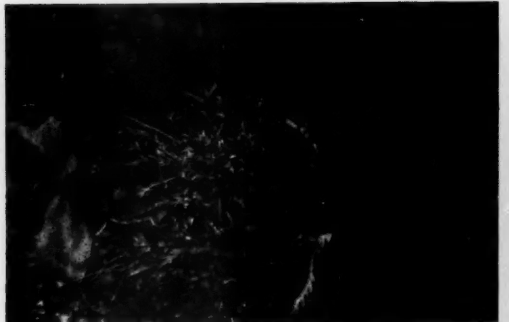
FIG. 9. Damage to cedar by deer browsing. Goldstream Lake.

Salal was present on 900 out of every 1,000 quadrats and in just over 40 per cent of these more than half the ground surface was occupied by the shrub.

In this plant community of the Goldstream area salal utilization was low—only 32 per cent of the plants were browsed and these lightly, seldom to more than 25 per cent of the annual growth. On other areas (e.g., Bald Mountain or the 1938 Goldstream burn) where second growth fir is less abundant the salal is cropped to a much greater degree.

In the case of species that did not occur at least 50 times on the 300 quadrats, the figures of browsing percentage are based upon a more extended recon-

naissance in which each such species is represented at least that number of times.

TREES AND SHRUBS OF THE GOLDSTREAM 1938 BURN AND THEIR UTILIZATION BY DEER

To facilitate more precise comparison of the various major habitats of the Goldstream area a census of trees and shrubs represented upon the 1938 burn on Goldstream Summit was conducted during the winter 1940-41. The technique applied was the same used in the prior study of the second growth fir area.

In this major habitat type it was found that approximately 9 per cent of the ground surface is barren. That is 9 per cent of the milacre quadrats bore no vegetational cover whatever, a further 2 per cent is sedge meadow or cedar bottom. The remaining 89 per cent is presumptive second growth forest land and at present supports a mesic flora providing deer browse.

It was not possible to census the deer population utilizing this area. Over much of the year the parts farthest removed from cover are relatively little utilized while those parts within a mile of standing timber are heavily browsed.

Figures of the numerical composition of the flora on a representative acre of this burn are given in Table 13. In comparison with Table 12 many differences will be noted.

TABLE 13. Available trees and shrubs per acre on the Goldstream 1938 burn and their utilization by deer.

Species	Total number of plants per acre	Number of quadrats (out of 1000) upon which species occurred	Browsing per cent
Pseudotsuga taxifolia	120	90	92%
Thuja plicata	60	50	100%
Tsuga heterophylla	120	60	0
Vaccinium parvifolium	10	10	100%
Struthiopteris spicant	100	40	70%
Polystichum munitum	250	170	75%
Rubus leucodermis	130	110	100%
Rubus macropetalus	50	48	40%
Ribes lobbii	20	18	0*
Ribes lacustre	10	15	0*
Rosa gymnocarpa	20	20	100%
Alnus rubra	30	20	0*
Chimaphila umbellata	50	20	0
Berberis nervosa	1770	370	29%

*Species upon which browsing is restricted to leaves and is not discernible during the winter.

The most abundant species on this habitat was salal. This shrub was present on 81 per cent of the quadrats counted and covered in the aggregate 30 per cent of the ground surface. Fifty per cent of the salal plants exhibited signs of browsing by deer.

Berberis nervosa was abundant, and averaged 1,770 plants per acre of which 520 or just under one third were browsed. This per cent utilization is almost identical with that occurring under significantly lighter concentrations in the 1922 second growth.

The hemlocks present consisted largely of young

growth surrounding sedge meadows. It was a residuum of a much denser growth present in the subclimax forest before logging and burning.

The majority of the one hundred and twenty Douglas firs per acre were new seedlings, many of them barely six inches in height. It is noteworthy that under these conditions of sparse fir growth the utilization by deer was significantly higher. Thus in the second growth burn with high fir concentration utilization was but 63 per cent whereas in the 1938 burn with low fir reproduction utilization was 92 per cent.

WOODY PLANTS AND FERNS OF THE CONIFEROUS SUBCLIMAX FOREST ON GOLDSTREAM SUMMIT AND THEIR UTILIZATION BY DEER

In the early spring of 1941 a census of trees and shrubs on the subclimax forest area was made to facilitate comparison of this major habitat with the other two types, viz., 1938 burn and second growth fir. Methods used were the same as in these other areas.

The forest cover, per acre, of this associes was found to consist of 170 mature Douglas firs, 30 cedars, 110 hemlocks over 15 feet in height, 3 balsam firs and 2 white pines.

The shade provided by a forest of this density restricts the number of species comprised in the undergrowth. The most abundant species was again salal. This shrub here occurred on 88 per cent of the quadrats examined and occupied approximately 42 per cent of the ground surface.

The incidence of browsing on salal in this habitat was found to be very small in comparison with that on the two more open habitats. In the sublimax forest only 1.6 per cent of the salal plants had been browsed while corresponding figures for the 1938 burn and second growth fir areas were 50 per cent and 30 per cent respectively. It is thought that either absence of other favored browse species in the mature forest or inferior palatability of salal grown in such forest is responsible for the slight browsing upon the plant in this habitat.

The complete list of woody plants encountered, their numerical density per acre and degree to which they were browsed is given in Table 14. It will be noted that while 250 young firs per acre were present these were all under 8 inches in height and had been ignored by the deer.

Comparison of Table 14 with Tables 13 and 12 will reveal the paucity of available browse plants in the forested habitat. The palatable species, Thuja, Rosa, Vaccinium and Berberis that showed heavy to moderate utilization were not only thinly distributed but by their habit of growth they are able to contribute little to the bulk of browse required by the deer population. Herbaceous plants are correspondingly scarce in this habitat and these factors, combined with the apparent unpalatability of the subforest salal further emphasize the inferiority of the conifer forest habitat as a feeding ground for deer.

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TABLE 14. Available woody plants per acre on Gold-stream subclimax forest and their utilization by deer.

Species	Total number of plants per acre	Number of quadrats (out of 1000) upon which species occurred	Browsing per cent
Pseudotsuga taxifolia 4″ to 8″.	250	120	4
Thuja plicata.................	90	60	100
Tsuga heterophylla............	210	140	0
Vaccinium parvifolium........	110	70	90
Alnus rubra..................	5	2	not shown
Salix sp.....................	10	8	not shown
Berberis nervosa.............	900	200	36
Ribes palustris..............	50	40	40
Ribes lobbii.................	10	10	0
Rubus macropetalus..........	50	50	not shown
Rosa gymnocarpa.............	100	30	90
Pinus monticola.............	5	5	0
Chimaphila umbellata........	240	20	0
Polystichum munitum........	30	20	33
Polystichum lonchitis........	5	5	0
Polypodium sp...............	10	3	0

FOOD HABITS OF COAST DEER AS DETERMINED BY STOMACH ANALYSIS

In the course of a study centered largely upon the investigation of parasites and diseases of the coast deer, a number of stomachs were collected throughout the years 1938 to 1940. In order that the stomachs might be in the best possible condition, all specimens collected by myself were where possible shot in the early morning before much remastication of the contents of the rumen had taken place. Specimens obtained from other sources had to be taken as they came. Stomachs of winter killed animals, dead of starvation, are not included here as under such circumstances the appetite may well be abnormal.

Stomach analysis is certainly the most satisfactory method of determining food habits. By this means a fairly accurate appraisal of the major dietetic items is possible. It is acknowledged, however, that it gives little indication of the scope of "snip browsing" on a wide variety of less abundant or less palatable plants. To determine this, stomach analysis must be supplemented by extensive field examinations of the food plants and observations of the living deer during their feeding activities.

From the type of vegetation consumed, determined largely by availability, it has been found possible to divide the feeding year into four seasons of unequal length. Thus in the Goldstream area the autumn browse period extends from early September until late November or early December—roughly a period of three months. During this period large quantities of deciduous vegetation are consumed, almost all of it the leaves of trees and shrubs. Thus it will be seen from Table 15 and Figure 10 that major food items during the autumn are alder, salal, and willow leaves supplemented by considerable quantities of mushrooms and some fir tips. Where low growing alders are available the leaves are stripped from the branches, leaving the petiole attached to the tree. Under other circumstances the newly fallen leaves
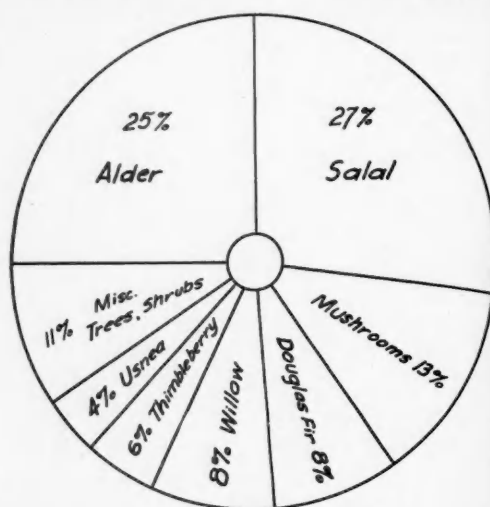
FIG. 10. Diagram of autumn foods of coast deer. The bulk contribution of each is expressed as a percentage.

are consumed. Browsing on the willow is not confined to leaves alone but twigs and buds also are taken.

The winter period on the Goldstream area is the longest of the four and extends from early December to mid April or over four and one half months. During these winter months food choice is very limited. The coast deer where I have studied it is not a twig eater and in consequence its primary winter food sources are the evergreen trees and shrubs (Fig. 11). In the fifteen winter stomachs examined tips

FIG. 11. Diagram of winter foods of coast deer.

TABLE 15. Important food items in stomachs of 40 deer from southern Vancouver Island listed seasonally; volume and number of occurrences expressed as percentages.

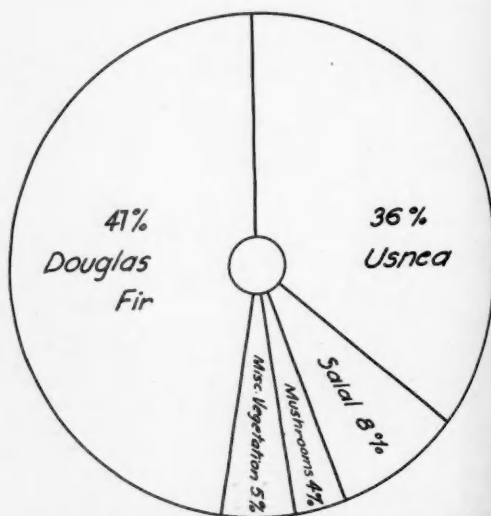| Season Number of stomachs Number of months in season		Autumn 15 3		Winter 15 4½		Spring 5 1½		Summer 5 3		Consumption index	
Common Name	Technical Name	Vol. %	Occ. %	Vol. %	Occ. %	Vol. %	Occ. %	Vol. %	Occ. %	Actual	%
Douglas fir	Pseudotsuga taxifolia	8	53	47	100	24	60	0	0	272	23
Salal	Gaultheria shallon	27	73	8	54	6	60	41	100	249	21
Old man's beard	Usnea barbata	4.4	34	36	100	0	0	0	0	162	14
Willow	Salix sp.	8	34	0	0	21	60	6	50	73	6
Alder	Alnus rubra	25	60	0	0	trace		14	60	117	10
Bracken	Pteris aquilina	1.5	13	0	0	11	80	4	20	33	3
Oregon grape	Berberis nervosa	trace	7	1	7	trace		0	0	5	.4
Dogwood	Cornus nuttallii	0	0	0	0	4	20	0	0	6	.5
Maple	Acer macrophyllum	1.0	20	0	0	4	20	0	0	9	.8
Madrone	Arbutus menziesii	2.1	7	0	0	0	0	0	0	6	.5
Spiraea	Spiraea discolor	2.1	7	0	0	0	0	0	0	6	.5
Cedar	Thuja plicata	1.5	20	2	30	trace	20	0	0	14	1
Thimbleberry	Rubus parviflora	6.2	20	0	0	0	0	0	0	19	2
Black-cap	Rubus leucoderma	0	0	0	0	0	0	9	40	27	2
Grass and sedge		trace	7	0	0	5	40	4	60	20	2
Horsetail	Equisetum pratense and arvense	0	0	0	0	12	40	0	0	18	2
Mushroom		13	53	4	20	0	0	0	0	57	5
Willow herb	Epilobium sp.	0	0	0	0	3	20	trace	0	5	.4
Cat's ear	Hypochaeris radicata	trace	8	0	0	1	20	0	0	2	.1
Flat lichen		trace	20	2	60	0	0	0	0	9	.8
Misc. and unidentified green plants		0	0	trace	7	9	100	25	100	88	8
TOTALS										1197	

and needles of Douglas fir comprised 47 per cent of the combined contents and the arboreal lichen *Usnea barbata,* abundant on the mature firs of the area yielded another 36 per cent. Considering the abundance of salal on the area its low consumption (8%) is remarkable. Apparently fir and usnea are both preferable. The snows and high winds of winter bring down a steady cascade of broken limbs and these the deer hunt out to devour the lichen. I have known wild deer to come trotting up to a place where a fir had just been felled and to commence feeding on the lichen in full view of the faller.

Restricted availability no doubt accounts for the reduced number of species represented in the winter stomachs (11) in comparison with the autumn stomachs (17) (Table 16).

The spring browse period is short. It extends from approximately mid April to late May, that is, through the period of lush growth, when many annual and perennial herbs are soft and succulent, and when the trees are adding their new growth. Fir is still the most important single food item (Fig. 12), but during this period only the new, light-green, growing tips are eaten. These are swallowed almost unmasticated. The new growth of willow and the succulent tips of sprouting bracken (still in the curl) and foliaceous Equisetum are also eaten extensively. It is at this time that most of the grass, rushes and sedges are browsed. Dogwood and maple are scarce at the altitude of the Goldstream area and consequently though highly palatable they are not an important food source.

TABLE 16. List of food plants taken from stomachs of coast deer on southern Vancouver Island, B. C., in fall and winter.

Species	FALL STOMACHS (15)		WINTER STOMACHS (15)	
	Number of occurrences	Parts eaten	Number of occurrences	Parts eaten
Pseudotsuga taxifolia	8	needles	15	needles
Gaultheria shallon	11	leaves	7	leaves
Alnus rubra	9	leaves	0	
Salix sp.	5	leaves and buds	0	
Usnea barbata	5	....	15	
Thuja plicata	3	leaves	5	leaves
Mushrooms	8	thallus	2	thallus
Flat lichen	3	....	7	
Rubus parviflora	3	leaves	0	
Pteris aquilina	2	leaves	0	
Acer macrophyllum	3	leaves	0	
Arbutus menziesii	1	leaves	0	
Spiraea discolor	1	leaves	0	
Symphoricarpos racemosa	1	leaves and fruit	0	
Berberis nervosa	1	leaves	1	
Grass	1	leaves		
Hypochaeris radicata	1	leaves	1	leaves
Selaginella sp.	0	....	1	
Rubus macropetalus	0	....	1	leaves
Carex sp.	0	....	1	

Only a small number of stomachs are available for the summer period (June 1 to August 31) but the results from these correlate well with those expected as a result of field observations (Fig. 13).

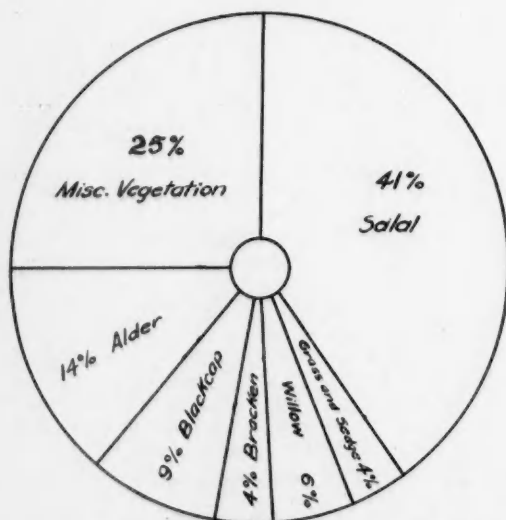Fig. 12. Diagram of spring foods of coast deer.

Fig. 13. Diagram of summer foods of coast deer.

The major food item in June is the new leaves of salal and in July and August the leaves and particularly the berries of this shrub are consumed in large quantities. When available the berries are the favored food and are frequently eaten almost exclusively. In one stomach examined 80 per cent of the contents consisted of salal berries, ripe and unripe.

The presence of clover in two of the four stomachs examined to an average bulk of 20 per cent of the total stomach contents is abnormal. These two deer were shot near some cultivated fields where clover abounded. Away from cultivation clover is scarce and its consumption by deer limited. Alder 7 per

cent, and willow 8 per cent of the stomach contents are characteristic of the summer period foods in the Goldstream area.

Bracken also is eaten in considerable amounts. In one stomach it represented 20 per cent of the contents.

In an effort to express numerically the relative importance of the more frequently eaten plants on the Goldstream area I have derived a somewhat artificial figure, *the consumption index.* This is obtained by multiplying the mean percentage volume of a plant in the stomach contents during a certain period by the number of months represented and summing the four figures so obtained. To facilitate comparison of these results with other similar studies the consumption index is also reduced to a percentage basis.

For example Douglas fir constituted 8% by volume of the autumn stomach contents, the autumn period is 3 months, $3 \times 8 = 24$. Similarly for the winter period, with a volume contribution of 47% over $4\frac{1}{2}$ months the index is 212. The spring contribution similarly derived is $24 \times 1\frac{1}{2} = 36$ and that of the summer $0 \times 3 = 0$. Summing these 4 seasonal contributions gives the consumption index for Douglas fir of 272 which when reduced to a percentage of the sum of all consumption indices, in this instance 1,197, amounts to 23% of the annual diet.

This figure, while limited in precision by the approximate nature of its components, provides a useful index of the relative bulk contribution of individual forage species to the annual deer browse. The figures derived for the Goldstream area will probably be approximately accurate throughout the same floral type, but will vary with the relative abundance of different plant species and with the variety of components in the plant community.

The consumption index does not necessarily indicate the relative food value of a given species from the standpoint of deer maintenance. Food value is dependent also upon the nutritive value of the plant. De Nio (1938) makes the statement that Douglas fir is comparable to Idaho fescue in per cent of carbohydrates, fats, proteins, ash, and crude fibre. This grass is considered to be a highly nutritive fodder plant. Thus in this instance, provided that the chemical constituents of Douglas fir are in an available form, it seems likely that the most abundant and favored browse species is also a highly nutritive one.

The consumption index makes possible a valuation of the relative contributions of different types of vegetation to the annual food of the coast deer. In the Goldstream area it can be seen that trees and shrubs contribute by far the largest element in the diet (Fig. 14). This source has a consumption index of 803 out of a total of 1,197 or roughly 67 per cent. Of this, 286 units (24%) represent conifer browse and 517 (43%) that supplied by deciduous trees and shrubs including salal and madrone in this group.

The second largest single food source is the arboreal lichens. These provide 171 units (14%). The high consumption of these lichens is apparently characteristic wherever they are available. Herbaceous
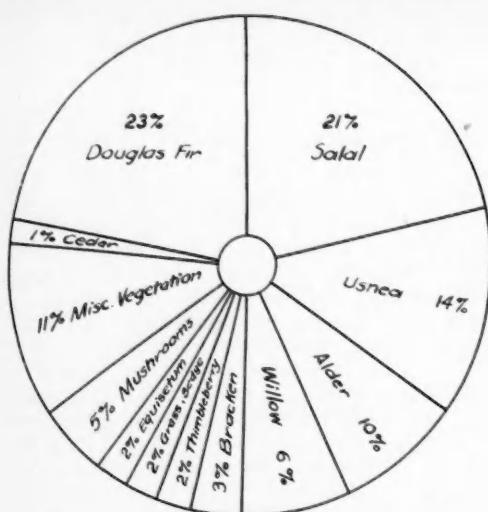
FIG. 14. Diagram of annual food of coast deer. The bulk contribution of each item is expressed as a percentage as derived from the consumption index.

plants with an index of 95 (8%), mushrooms with 57 (5%), ferns and horsetails with 51 (5%) and grasses, sedges and rushes with an index of 20 (2%) are of minor browse importance from the standpoint of bulk contribution. It is quite possible however that certain of these minor items possess nutritional elements out of all proportion to their bulk consumption and are of vital importance in the diet.

From the foregoing it will be evident that the coast deer is a browsing species and that low growing vegetation is eaten in but limited amounts.

THE COAST DEER AND THE DOUGLAS FIR

It has been shown that in the study areas Douglas fir as represented by young trees is the most important single food item in the annual diet of the coast deer. This tree is also the most important single timber tree in British Columbia. Thus the impact between this tree and the coast deer is of considerable importance.

In the Goldstream area second growth Douglas fir occurs in uneven stands. In the salal bottoms and the sedge meadows firs do not usually grow, though there may be occasional trees in the former. The thinnest stands of fir are those on the rock bluffs. Here only in gullies and crannies is there sufficient depth of soil and constancy of soil moisture for this conifer. Other marginal areas such as the borders of sedge meadows are likewise thinly stocked.

As has already been stated the coast deer in its feeding avoids very dense cover if possible. This is reflected in the figures of density of stand as related to percentage of trees browsed, presented in Table 17. It will be seen that the heaviest browsing takes place upon quadrats supporting from 1 to 3 trees. There is reduced, but fairly uniform, utilization on

quadrats bearing 4 to 12 trees but at concentrations more dense than that, 13 to 42 trees per quadrat, the percentage utilization becomes progressively less.

TABLE 17. Browse intensity related to density of stand of second growth Douglas fir in the Goldstream area.

Trees per quadrat	Number of quadrats	Percentage of trees browsed
1 - 3	77	80%
4 - 6	53	69%
7 - 9	17	78%
10 - 12	5	67%
13 - 15	5	49%
16 - 18	5	38%
19 - 42	5	25%

*Quadrats bearing any "yellow" trees not included.

As a matter of fact the difference is even more pronounced than is shown by the table for the trees on the thinly forested quadrats are individually more heavily browsed than are the browsed trees where the stand is heavier.

From this it will be seen that the influence of deer upon regenerating fir depends not only upon the density of the deer population but to a great extent also on the density of the second growth trees. This in turn is influenced by many factors, a large percentage of them uncontrollable.

Under ordinary circumstances the logging of a virgin subclimax fir forest leaves an area very thinly populated with deer. If satisfactory seeding takes place within a year or two the regenerating fir may be well started before the deer population builds up. In fact the ability of the deer population to increase under such conditions on Vancouver Island is often dependent in no small part on the stand of young Douglas firs.

Any consideration of the economic importance of deer in a second growth fir forest involves the expected yield of mature trees upon the area in question.

According to yield tables published by the British Columbia Forest Service (1936) expected yield of Douglas fir after 100 years under maximum seeding conditions varies from 400 trees per acre on poor sites with an index of 50 feet at 100 years to 50 trees per acre on the best sites with an index of 170 feet at 100 years. Under good natural seeding conditions 20 thousand or more seedlings per acre may start. Such a seedling density will have few milacre areas supporting less than 20 trees and in consequence under existing browse pressure of 20-30 deer per square mile, serious browsing, involving removal of the leader should not be in excess of 40 per cent and will probably be less than 20 per cent.

It is obvious that even on poor sites, if well seeded, such deer browsing will have little or no deleterious effect on quality or quantity of the final yield.

On the other hand current artificial reforestation practice calls for the planting of approximately 1,200 trees per acre, spaced roughly 6 feet by 6 feet. Such

reforestation is frequently undertaken on old burns not restocking satisfactorily and already supporting a good population of deer. The planting procedure insures that there will not be in excess of 2 trees per milacre. Consequently no protection is derived from the observed reluctance of deer to browse the central trees of dense stands. Under such conditions maximum depredation can be expected.

Under present reforestation practice, if a good site is involved, tree growth is rapid and only a small number of surviving trees are required to provide an adequate forest cover. On such sites a normal deer population has little apparent deleterious effect. However upon poor sites where growth is slow and expected yield in number of trees is high, normal deer populations have a marked deleterious action and may upon occasion almost eliminate the regenerating fir forest and leave the remaining trees limby and with a reduced timber value.

So far as winter browse is concerned there are very few buffer species on Vancouver Island that can be used to protect young firs. Cedar is usually browsed in preference to fir where both are available but cost together with the rather strict habitat requirements of cedars render their use as a buffer impracticable.

Three alternatives appear as theoretical means of preventing serious damage to fir plantations upon suboptimum sites.

1. Removal of the deer.

2. Treating the trees to render them unpalatable.

3. Modification of planting practice.

The first alternative is highly inadvisable from the political standpoint and short sighted also inasmuch as in any integrated land use program the game should be considered as the annual income derived from the land between the widely separated periods of income that results from harvesting the forest.

No effective method has yet been devised for producing permanent unpalatability in young conifers. The differential utilization of the yellow trees as compared with the green trees, that I have remarked on elsewhere in this paper suggests a method of accomplishing this end that might bear further investigation.

Two modifications of current reforestation practice suggest themselves. To take advantage of the inhibiting effect of density of stand upon the browsing of conifers by deer, groups of buffer trees of the same species might be planted around a selected number of the seedling transplants. The cost factor, however, may well render such a program impracticable.

Perhaps the most satisfactory method of obtaining a forest yield from suboptimal land in the face of a normal or large deer population is to plant western hemlock alone in such localities. A program of this nature would tend to materially reduce the value of the land for hunting purposes, but should provide rapid reforestation unimpeded by deer damage.

Young hemlock seedlings under 18 inches in height may suffer serious damage from sooty grouse (Den-dragapus fuliginosus) where such are abundant during their breeding season, but on Vancouver Island at least there are no other known vertebrate foragers upon this tree.

WATER AND MINERAL CONSUMPTION

The consumption of water by coast deer varies much throughout the year. During the winter months I have only once observed deer drinking water as such. It is quite possible however that they eat a certain amount of snow when it is available.

In the area under consideration the winter and early spring are very wet and probably all the necessary water is obtained incidental to normal feeding activity.

On the other hand the summers are warm and dry and though heavy dews are frequent the vegetation becomes progressively desiccated. For this reason, as well as to fill the increased water needs incident to maintaining the body temperature, the deer drink frequently during the summer months.

It was usual to observe deer at water toward the end of the morning period of feeding. In July and August many deer were observed at water between 7 a.m. and 8 a.m., some between 8 a.m. and 9 a.m. but few after that until about noon.

At Bald Mountain in July and August, 1940, there was a pronounced early afternoon movement to water on the part of deer bedded within easy reach of such. However the deer bedded on the rocky slopes and rolling burned land a quarter of a mile or more from the lakeshore did not drink at this time.

On this same area the evening browsing period in mid August began between 5:00 and 5:30. On August 26, 1939, the temperature reached a high of 86° F. At 5:30 p.m. from an observation post on the lakeside trail I watched two large bucks and a doe commence feeding in the bracken-filled gullies near the crest of the hill. At 6:00 p.m. on the same date a doe and fawn were watched as they came down the hill and made their way to water. At 6:25 the sun went down, tabanids were still on the wing but since 5:30 or so had not been bothering the deer. By 6:30 p.m. dusk was gathering fast and there was pronounced activity beginning among the deer on the hillside. By standing in one place I was able to watch, within 40 minutes of sundown, 10 deer, all does and young animals, including 2 spike bucks move down off the hill to drink at the lake. Neither of the large bucks had descended before it became too dark to see them. Some of the deer moved at a trot and drank avidly as if their thirst was extreme. Thus it will be seen that during the warm summer weather at least there is a pronounced evening movement to water just after sundown. Early morning observations revealed a similar but less pronounced movement to water before progress to the bedding grounds began.

Nowhere in the British Columbia range of the coast deer have I found places which the deer were using as "licks." Possibly the abundant rainfall serves to

leach out such readily soluble mineral matter as is attractive to the deer. Over large parts of the area inhabited by this species the deer live their entire lives without access to minerals other than what they ingest in their food and water.

Where deer are residing within easy reach of tide-water beaches, however, the normal mineral intake is frequently supplemented by licking the accumulated rime from rocks, also by eating appreciable quantities of algae. From the stomachs of deer shot on beaches of some of the northern islands I have recovered leaves of kelp (Macrocystis and Nereocystis) and sea lettuce (Ulva) in some quantities and I have seen indications on the beach near Comox, Vancouver Island, that suggested the deer were eating Fucus there.

These visits to the beaches are usually confined to the night and consequently it is difficult to observe the behaviour of the animals but the evidence from tracks indicates that the deer actually wade into the salt water. I do not know whether or not they ever drink it.

In the Goldstream Lake area of Vancouver Island shed antlers and skeletons of deer are consumed as soon as they become sufficiently weathered for the deer to eat. Skeletons seldom last as long as two years except for some of the harder parts of the cranium and the long bones. This no doubt indicates a craving for calcium phosphate that cannot be satisfied in any other way.

Another local habit is that of eating fresh wood ash and charcoal. It is a common sight after a forest fire to see deer eating the ashes, often still warm, and I have watched deer removing and eating the charcoal from stumps and logs burned many years before. The removal is accomplished with the lower front teeth, used with an unward motion of the head and neck.

Inasmuch as charcoal is a recognized vehicle used in treating certain types of nutritional anaemia and mineral deficiency in domestic stock it is doubtless a valuable addition to the diet of the deer. The observed preference for fresh charcoal over that for charcoal several years old may be explained by the greater richness of the former in water soluble minerals.

Pebbles are of frequent occurence in the stomachs of deer but I doubt that they are ingested purposely. My observations suggest that they are taken accidentally during feeding and drinking activity.

Bark, particularly of Douglas fir was found frequently in stomachs from the Goldstream Lake area. The same stomachs invariably contained quantities of arboreal lichens that grow on fir trees and it is thought that the bark was taken accidentally while stripping the lichens.

DISCUSSION OF FOOD PLANTS AND THE EFFECT UPON THEM OF DEER BROWSING

In Tables 18, 19, 20 and 21 are listed the plants of southern Vancouver Island, insofar as I have observed their status as deer food. I have separated them into highly palatable species, moderately palatable species, plants of low palatability and plants not observed to be eaten by wild deer. In accomplishing this subdivision I have used as a criterion the selective browsing of the plant species. If a high proportion of the individual plants of a species are browsed under normal population pressure the plant is listed as highly palatable. If there is no sign of special seeking for a certain plant and as a result only a small proportion, say less than one third of the plants, show signs of deer browsing the species is judged as moderately palatable. Other plants are browsed only very occasionally even when abundant perhaps not more than one in fifty plants have been browsed and these usually but slightly. Such plants are included in the list of those of low palatability. The list of plants not eaten by deer includes many species that were tested on deer in confinement after prolonged observation in the wild had failed to establish any utilization. It also includes certain sedges and grasses that further study may show to be snip-browsed occasionally when young.

I have adopted this method of indicating palatability, which is similar to that used by Dixon (1934) in preference to any attempt to assign a numerical rating for reasons set forth in the introduction.

Deer browsing on certain preferred plants can at times become a serious menace to the spread or even the survival of such plants. Thus overpopulation by deer will tend gradually to eliminate the available preferred species and to reduce correspondingly the carrying capacity of the range.

Where plant species included in the accompanying lists of slightly palatable or unpalatable species are being utilized extensively and where, at the same time, the preferred browse species are badly damaged or reduced in number, serious overpopulation exists and heavy winter losses can be expected.

TREES AND SHRUBS

Madrone (*Arbutus menziesii*). This tree is abundant at low elevations on southeastern Vancouver Island, and wherever it exists in fair numbers it is a major food species during the winter (Fig. 15). At Bald Mountain reserve it is heavily browsed from October until March. By the end of this period almost 100 per cent of the available leaves have been removed. In March the new growth begins but it is not touched by the deer. As a result of this type of utilization the trees are damaged very little. By the end of the summer the new twig growth has become woody and unpalatable so that usually only

TABLE 18. Plants of southern Vancouver Island highly palatable to deer.

Common Name	Technical Name	Parts eaten—Remarks
TREES AND SHRUBS		
Vine maple	Acer circinatum Pursh	Leaves all summer.
Smooth maple	Acer glabrum Torr	Leaves all summer; shed leaves fall.
Red alder	Alnus rubra Bong	Leaves, late summer; shed leaves fall.
Service berry	Amelanchier florida Lindl.	Leaves, summer, fruit summer.

TABLE 18. *(Continued)*

Common Name	Technical Name	Parts eaten—Remarks
Madrone	Arbutus menziesii Pursh	Leaves, late fall and winter.
Flowering dogwood	Cornus nuttallii T. & G.	Leaves all summer. Twigs winter and spring.
Western dogwood	Cornus pubescens Nutt.	Leaves all summer; twigs late winter; fruit.
Hawthorn	Crataegus brevispina (Doug.) Heller	Leaves, spring and summer.
Hawthorn	Crataegus oxycantha L.	Leaves, spring and summer.
Salal	Gaultheria shallon Pursh	Leaves fall, winter, spring; berries, summer.
Bird cherry	Nuttallia cerasiformis T. & G.	Leaves, spring and summer.
Mock orange	Philadelphus gordonianus Lindl.	Leaves, spring and summer.
Douglas fir	Pseudotsuga taxifolia (Lamb.) Britt.	Branch tips, winter; new growth spring.
Crab apple	Pyrus diversifolia Bong.	Leaves summer and early fall.
Garry oak	Quercus garryana Dougl.	Leaves late summer; acorns fall.
Flowering currant	Ribes sanguinea Pursh	Leaves, spring and summer.
Black raspberry	Rubus leucodermis Dougl.	Leaves, summer.
Willow	Salix geyeriana Anders.	Leaves all summer, twigs winter and spring.
Willow	Salix lasiandra Benth.	Leaves all summer.
Willow	Salix scouleriana Hook.	Leaves all summer.
Willow	Salix sitchensis Bong.	Leaves all summer, buds and flowers, spring.
Red elder	Sambucus racemosus L.	Leaves, spring and summer.
Buffalo berry	Shepherdia canadensis Nutt.	Leaves, midsummer.
Ocean spray	Spiraea discolor Pursh.	Leaves, all summer.
Giant cedar	Thuja plicata Donn.	Leaves, winter and early spring.
Red huckleberry	Vaccinium parvifolium Smith	Leaves, twigs and berries.
HERBACEOUS PLANTS		
Wild onion	Allium cernuum Roth	In late spring, young shoots.
Camas	Camassia quamish Greene	Leaves, spring.
Bitter cress	Cardamine breweri Wats.	Flower heads.
Field chickweed	Cerastium arvense L.	
Cat's ear	Hypochoeris radicata L.	Leaves, winter, spring; leaves and flowers, summer and fall.
Canada mint	Mentha canadensis L.	Leaves.
Musk	Mimulus moschatus Dougl.	Eaten avidly in early spring where it is aquatic. Roots and stems.
Spring beauty	Montia parviflora (Dougl.) Howell	Leaves, stems and flowers.
Water parsley	Oenanthe sarmentosa Presl.	Leaves and stems.
Wintergreen	Pyrola picta Smith	Leaves and flowers.
Creeping buttercup	Ranunculus flammula var. reptans Mey.	Leaves and stems, early spring.
Hedge nettle	Stachys ciliata Dougl.	Leaves.
GRASSES, SEDGES, AND RUSHES		
Sweet vernal grass	Anthoxanthum odoratum L.	Leaves, spring, summer and fall.
Sedge	Carex kelloggii Boott.	Leaves, spring and summer.
Sedge	Carex oederi Retz.	Leaves, spring and summer.
Indian reed grass	Cinna latifolia (Torr.) Grisch.	Leaves, spring and summer and fall.
Manna grass	Glyceria striata (Lamb.) Hitch.	Leaves, spring, summer and fall.
Flowering rush	Juncus ensifolius Wiks.	Leaves, spring.
FERNS, EQUISETUMS, ETC.		
Yellow boletus	Boletus subaureus	Fruiting bodies, fall and winter
	Boletus sp.	Fruiting bodies, fall and winter.
Giant clitocybe	Clitocybe gigantea	Fruiting bodies, October.
Morel	Morchella esculenta	Fruiting bodies, early spring.
	Russula atropurpurea	Fruiting bodies, fall.
Old man's beard	Usnea barbata	Winter.

TABLE 19. Plants of southern Vancouver Island moderately palatable to deer.

Common Name	Technical Name	Parts eaten—Remarks
TREES AND SHRUBS		
White fir	Abies grandis Lindl.	Branch tips, late winter,
Broad-leaved maple	Acer macrophyllum Pursh.	Leaves spring and summer. shed in fall.
Slide alder	Alnus sitchensis (Regel.) Sarg.	Leaves summer and fall.
Tall Oregon grape	Berberis aquifolium Pursh.	Leaves, winter; new growth, spring.
Oregon grape	Berberis nervosa Pursh.	Leaves, winter; new growth, spring.
Broom	Cytisus scoparius Link.	Flowers and leaves, spring, summer and winter.
Orange honeysuckle	Lonicera ciliosa Poir.	Leaves spring and summer.
Fly honeysuckle	Lonicera involucrata Banks.	Leaves spring and summer.
Aspen	Populus tremuloides Michx.	Leaves summer and fall.
Black poplar	Populus trichocarpa T. & G.	Leaves summer and fall.
Small brier	Rosa gymnocarpa Nutt.	Leaves spring to fall; fruit fall and winter.
Nootka brier	Rosa nutkana Presl.	Leaves spring to fall; fruit fall and winter.
Trailing blackberry	Rubus macropetalus Dougl.	Leaves summer, fall and winter.
Thimbleberry	Rubus parviflorus Nutt.	Leaves summer.
Salmonberry	Rubus spectabilis Pursh.	Leaves summer.
Hardhack	Spiraea douglasii Hook.	Leaves summer.
Snowberry (Waxberry)	Symphoricarpos racemosa Michx.	Berries fall and winter; leaves summer.
HERBACEOUS PLANTS		
False dandelion	Agoseris laciniata (Nutt.) Greene.	Leaves and flowers, early spring.
Bitter cress	Cardamine kamtschatica Schultz.	Early spring.
Bitter cress	Cardamine oligosperma Nutt.	Very early spring.
Hawk's beard	Crepis biennis L.	Summer.
Willow herb	Epilobium adenocaulon Haus.	Spring and summer.
Fireweed	Epilobium angustifolium L.	Late spring and summer.
Bird-foot clover	Hosackia parviflora Benth.	Leaves and stems spring.
Plantain	Plantago maritima L.	Spring and summer.
Dandelion	Taraxacum officinale L.	Early spring.
Red clover	Trifolium pratense L.	Leaves, summer.
White clover	Trifolium repens L.	Leaves, summer.
GRASSES, SEDGES AND RUSHES		
Wheat grass	Agropyron pauciflorum (Schwein.) Hitch.	Leaves, spring.
Bent grass	Agrostis exarata Trin.	Leaves, spring.
Brome grass	Bromus vulgaris (Hook.) Shear.	Leaves, spring.
Wild rye	Elymus glaucus Buck.	Leaves, spring.
Red Fescue	Festuca rubra L.	Leaves, spring.
Wood rush	Luzula campestris (L.) DC.	Leaves, spring.
Wood rush	Luzula parviflora Desv.	Leaves, spring.
FERNS, EQUISETUMS, ETC.		
Common horsetail	Equisetum arvense L.	Spring, foliaceous plants.
Kelp	Macrocystis sp.	All seasons.
Kelp	Nereocystis sp.	All seasons.
Sword fern	Polystichum munitum var. imbricans (D.C.) Eaton.	Summer, new growth.
Cliff brake	Pellaea densa (Brack.) Hook.	Summer.
Bracken	Pteris aquilina L.	New shoots (spring), tips summer and fall.
Mushroom	Tricholoma ? personatum	
Sea lettuce	Ulva sp.	All seasons.

TABLE 20. Plants of southern Vancouver Island eaten by deer casually or under stress (slight palatability).

Common Name	Technical Name	Parts eaten—Remarks
TREES AND SHRUBS		
Manzanita	Arctostaphylos columbiana Piper	Leaves, winter.
Manzanita	Arctostaphylos media Greene	Leaves, winter and fall.
Manzanita	Arctostaphylos tomentosa Dougl	Leaves, winter.
Bearberry	Arctostaphylos uva-ursi	Leaves, winter.
Rocky Mountain juniper	Juniperus scopulorum Sarg	Branch tips, winter.
Labrador tea	Ledum groenlandicum Oeder	Leaves, winter.
Sitka spruce	Picea sitchensis Carr	New growth, early spring.
Western white pine	Pinus monticola Dougl	Needles, late winter.
Rhododendron	Rhododendron californicum Hook	Leaves, winter.
Swamp gooseberry	Ribes lacustre Poir	Leaves and fruit, spring to fall.
Lobb's gooseberry	Ribes lobbii Gray	Leaves and fruit late summer.
Oregon yew	Taxus brevifolia Nutt	Branch tips, winter.
Evergreen huckleberry	Vaccinium ovatum Pursh	New leaves.
HERBACEOUS PLANTS		
Yarrow	Achillea millefolium L	Flowers, summer.
May leaves	Achlys triphylla DC	Leaves, late summer.
Silver green	Adenocaulon bicolor Hook	leaves, summer.
	Boykinia occidentalis T. & G	Leaves and flower heads, early summer.
Shepherd's purse	Capsella bursa-pastoris (L.) Medic	Leaves, summer.
Canada thistle	Carduus arvensis (L.) Scop	New leaves, early summer.
Edible thistle	Carduus edulis Greene	Leaves, early spring.
Mouse-eared chickweed	Cerastium viscosum L	Leaves, spring.
Prince's pine	Chimaphila umbellata (L.) Nutt	Leaves, late winter.
Larkspur	Delphinium menziesii DC	Leaves and stems, spring and summer.
Alpine willowherb	Epilobium alpinum L	Leaves and tips, early spring.
Willowherb	Epilobium minutum Lindl	Leaves, spring and summer.
Horseweed	Erigeron canadensis L	Leaves and stems, summer.
Cleavers	Galium aparine L	Leaves and stems, spring.
Bedstraw	Galium biflorum Wats	Leaves and flowers, early spring.
Sweet scented bedstraw	Galium triflorum Michx	New growth, spring and summer.
Dove's-foot geranium	Geranium molle L	Leaves, summer (captive animal).
Large-leaved yellow avens	Geum macrophyllum Willd	Leaves, spring.
	Gilia heterophylla Hook	Early spring.
Alum root	Heuchera micrantha Willd	Leaves, spring and summer.
Hawkweed	Hieraceum albiflorum Hook	Leaves, summer.
Lettuce	Lactuca muralis (L.) Fresen	Leaves, summer.
Twayblade	Listera nephrophylla Rydb	Entire plant, summer.
Indian consumption plant	Lomatium nudicaule Pursh	Eaten on 1 occasion (captive deer).
Blue lupine	Lupinus latifolius sep	Leaves, summer.
Skunk cabbage	Lysichiton kamtschatcense Schott	Leaf tips, early spring.
Buckbean	Menyanthes trifoliata L	Leaves, spring and summer.
Mitrewort	Mitella ovalis Greene	Leaves and stems, spring.
Mitrewort	Mitella pentandra Hook	Leaves and flowers, early spring.
Spring beauty	Montia sibirica (L.) Howell	Leaves, late spring.
Grove lover	Nemophila parviflora Dougl	
Lesser paint brush	Orthocarpus pusillus Benth	Leaves and flowers, spring.
Sweet Cicely	Osmorrhiza divaricata Nutt	Leaves, summer.
Colt's foot	Petasites speciosa (Nutt.) Piper	Leaves except for ribs, late summer.
Water crowfoot	Ranunculus aquatilis L	Surface tips, summer.
Sanicle	Sanicula menziesii Hook	
Spring sow thistle	Sonchus asper (L.) Hill	New leaves, summer.

Common Name	Technical Name	Parts eaten—Remarks
Chickweed	Stellaria crispa C. & S	Entire plant, summer.
False mitrewort	Tiarella laciniata Hook	Leaves and stems, spring and summer.
False mitrewort	Tiarella trifoliata L	Leaves and stems, spring.
	Tolmiea menziesii Pursh	Leaves, summer.
Western nettle	Urtica lyallii Wats	Only after frosting or withering.
False hellebore	Veratrum viride Ait	Leaves after frosting.
Pea-vine	Vicia americana Muhl	Leaves and stems, summer.
Spring vetch	Vicia sativa L	Summer, leaves.
GRASSES, SEDGES AND RUSHES		
Early hair grass	Aira praecox L	Leaves very early spring before flower heads come.
Hair grass	Agrostis hyemalis (Walt.) B.S.P	New growth, spring and summer.
Brome grass	Bromus carinatus H. & A	Early winter.
Brome grass	Bromus pacificus Shear	Early winter.
Sedge	Carex brunnescens Poir	New growth, sprg. and summer.
Sedge	Carex interior Bailey	New growth, sprg. and summer.
Sedge	Carex leersii Willd	New growth, sprg. and summer.
Sedge	Carex retrosa Schwein	New growth, sprg. and summer.
Sedge	Carex sitchensis Bong	New growth, sprg. and summer.
Rush	Juncus acuminatus Michx	
MISCELLANEOUS PLANT TYPES		
Maiden hair fern	Adiantum pedatum L	Leaves, summer.
Spleenwort	Asplenium felix-foemina (L.) Bernh	New leaves, early spring.
Scouring rush	Equisetum hyemale L	Young shoots, summer.
Stag-horn moss	Lycopodium annotinum L	Late winter and early spring.
Golden-backed fern	Pityrogramma triangularis (Kaul.) Maxon	Late winter.
Sword fern	Polystichum munitum (Kaulf.) Underw	Leaf tips late winter; a starvation diet.
	Selaginella sp	Accidental, one instance.
Deer fern	Struthiopteris spicant (L.) Hoffin	New growth summer; old growth, winter.

the leaves are removed during the winter. Certain trees, particularly those growing on rock bluffs and stunted as a result, show some damage. On overstocked areas such as the Bald Mountain reserve, where the population is in the vicinity of 40 deer to the square mile, the basal branches are damaged. The red alder *(Alnus rubra)* is subjected to very similar utilization. Almost no twig-browsing takes place in spite of heavy browsing on the leaves in late summer. In the autumn the fallen leaves are eaten in large quantities. Much the same applies to the maples *Acer glabrum* and *A. macrophyllum*, though in the latter species at least the reduced palatability is partly responsible for the lack of damage to the woody part of the tree.

The willows (Salix sp.), ocean spray *(Spiraea discolor)* and the dogwoods *(Cornus nuttallii* and *C. pubescens)* are all favored spring and summer browse species. With these the browsing extends to the twigs as well as the leaves and the trees are often seriously damaged. Individual dogwoods on the Bald Mountain reserve were so severely cropped that flowers were not produced during the three years I had the area under observation.

The acorns of the Garry oak *(Quercus garryana)* are a sought after food item in the autumn months. Apparently the acorns of this oak have a constipating effect if eaten in quantity. Two cases have

TABLE 21. Plants of southern Vancouver Island apparently not eaten by deer.

Common Name	Technical Name	Not eaten—Remarks
TREES AND SHRUBS		
Devil's club	Fatsia horrida (Sm.) B. & H.	Abundant in shaded wet spots.
Sheep laurel	Kalmia polifolia Wang.	Not common.
Scrub (Jack) pine	Pinus contorta Dougl.	Abundant locally.
Mountain rhododendron	Rhododendron albiflorum Hook.	Abundant at 2500 feet +.
Western hemlock	Tsuga heterophylla Sarg.	Abundant.
HERBACEOUS PLANTS		
False dandelion	Agoseris heterophylla (T. & G.) Greene.	Not common.
Douglas' aster	Aster douglasii Lindl.	Abundant in sedge meadow.
Pearly everlasting	Anaphalis margaritaceae Beuth.	Common.
Everlasting	Antennaria eximia Greene.	Casual.
Hairy rock cress	Arabis hirsuta (L.) Scop.	Casual on rock bluffs.
Wintercress	Barbarea vulgaris R. Br.	Abundant in early spring.
Common thistle	Carduus lanceolatus L.	Abundant in early spring and summer.
Bleeding heart	Dicentra formosa DC.	Rare, only 3 plants examined.
Swamp Gentian	Gentiana sceptrum Pall.	Abundant in swamps.
Cudweed	Gnaphalium palustre Nutt.	Scarce.
Cudweed	Gnaphalium purpureum L.	Scarce.
Mossy St. John's wort	Hypericum bryophytum Greene.	Dominant in sedge meadows.
Swamp St. John's wort	Hypericum scouleri Hook.	Abundant in some sedge meadows.
Twin flower	Linnaea borealis L.	Abundant.
	Luina hypoleuca Benth.	Rare, on dry hillsides.
Tarweed	Madia exigua (Smith). Greene.	Abundant on rock bluffs.
Yerba Buena	Micromeria douglasii Benth.	Fairly common.
Musk	Mimulus alsinoides Dougl.	Abundant on rock bluffs.
Musk	Mimulus langsdorfii Donn.	Abundant on rock bluffs.
Spring beauty	Montia parvifolia (Dougl.) Howell.	Dominant on rock bluffs.
Cow lilly	Nymphaea polysepala (Englm.) Greene.	Usually not available because of deep water.
Buttercup	Ranunculus bongardi Greene.	Rare.
Sorrel	Rumex acetosella L.	Abundant on new burns.
Burnet	Sanguisorba microcephalum Presl.	
Saxifrage	Saxifraga rufidula (Small.)	Casual.
Ragwort	Senecio triangularis Hook.	Only two plants seen.
Ragwort	Senecio fastigiatus Nutt.	Casual.
Groundsel	Senecio sylvaticus L.	Casual.
Marsh skullcap	Scutellaria galericulata L.	Casual.
Arctic star flower	Trientalis arctica Fisch.	Abundant in sedge meadows.
Hop clover	Trifolium agrarium L.	Abundant on rocky areas.
Sea blush	Valerianella congesta DC.	Abundant on rocky areas.
Brookline	Veronica americana Schwein.	Abundant.
Marsh speedwell	Veronica scutellata L.	Dominant in marshes.
Purple violet	Viola adunca Smith.	Casual.
Swamp violet	Viola palustris L.	Casual
Evergreen violet	Viola sempervirens Greene.	Abundant.
Poison camas	Zygadenus venosus Wats.	Casual.
GRASSES, SEDGES, RUSHES, ETC.		
	Agrostis stolonifera L.	
	Agrostis palustris Hitch.	
Silver hair-grass	Aira caryophyllea L.	Dominant on rock bluffs.
Sedge	Carex aquatilis Wahl.	Casual in sedge meadows.
Sedge	Carex stipata Muhl.	Casual in sedge meadows.
Sedge	Carex siccata Dewey.	Casual in sedge meadows.
Tufted hair grass	Deschampsia caespitosa R. Br.	Abundant in swamps.
	Dulichium arundinaceum (L.) Britt.	Common on mudflat.
Spike rush	Eleocharis palustris (L.) R. & S.	Scarce on mudflat.
Fescue grass	Festuca megalura Nutt.	

Common Name	Technical Name	Not eaten—Remarks
Fescue grass	Festuca occidentalis Hook.	
Oregon rush	Juncus oreganus Wats.	Abundant on mudflat.
Rush	Juncus tenuis Willd.	
Bugle weed	Lycopus uniflorus Michx.	Common on mudflat.
June grass	Poa pratensis L.	Common.
	Rhynchospora alba (L.) Vahl.	Common on mudflat.
Bull rush	Scirpus occidentalis (Wats.) Chase.	Scarce.
Bur-reed	Sparganium simplex Huds.	Casual.
Cat-tail	Typha latifolia L.	Scarce.
FERNS		
Spleenwort	Asplenium trichomanes L.	Scarce.
Grape fern	Botrychium silaifolium Presl.	
Bladder fern	Cystopteris fragilis (L.) Bernh.	Usually inaccessible.
Holly fern	Polystichum lonchitis (L.) Roth.	Usually inaccessible.

FIG. 15. *Arbutus menziesii* on Bald Mountain. Photographed Feb. 18.

been brought to my attention of deer in confinement developing serious constipation after feeding heavily on these nuts. In the late summer and autumn the leaves of this oak are frequently eaten in considerable quantities but no damage to the trees has been observed.

Salal *(Gaultheria shallon)* because of its high palatability and great range of climatic tolerance is one of the most important, if not the most important, browse species in southern British Columbia. In the west coast rain forests where this shrub grows to a height of fifteen feet or more and produces stems seven and eight inches thick much of the foliage is out of reach. But on eastern Vancouver Island where the usual height is two to four feet both foliage and fruit are readily available. Under browse pressure existing in the Goldstream area only moderate utilization of the abundant fruit crop occurs; but on the fully stocked Bald Mountain reserve I have found areas of an acre or more in which not a berry had escaped the combined onslaught of deer and sooty grouse.

Germination tests conducted with salal seeds recovered from feces removed from the colon of the deer have shown an average germination of 5 per cent. Absence of figures for natural germination prohibits comparison but this low viability is undoubtedly due in large part to the high percentage of unripe fruit eaten. That germination of salal seeds is possible after passage through the digestive tube involves the deer in the distribution of this plant to new areas.

The flowering currant *(Ribes sanguinea)* and red-berried huckleberry *(Vaccinium parvifolium)* are the two most heavily utilized and seriously damaged shrubs on southern Vancouver Island (Fig. 16). It

FIG. 16. *Vaccinium parvifolium* showing typical condition resulting from overbrowsing.

is estimated that a deer concentration of twenty-five per square mile will reduce the fruiting of these shrubs by as much as 90 per cent and that forty deer per square mile will almost eliminate flowering and fruiting of available plants of both species. Certain thorny shrubs are apparently highly palatable but suffer little or no serious damage, apparently because of the protection of their thorns. In this class are *Rubus leucodermis, Rosa nutkana,* and *R. gymnocarpa.*

The fruits of all these species are eaten with relish. Other fruits that I have observed deer eating, or have removed from their stomachs are *Ribes lobbii, R. lacustre, Rubus spectabilis, Amelanchier florida* and *Symphoricarpus racemosa.* Of these I have recovered viable Amelanchier and *Rubus spectabilis* seeds from deer feces and it is probable that germination of seeds of most, if not all these species is possible after passage through the digestive tract of the coast deer.

AQUATIC PLANTS

In the Goldstream area a number of aquatic plants were eaten with avidity. In certain marshy ponds and along a small stream water parsley *(Oenanthe sarmentosa)* and the buttercup *Ranunculus repens* were dominant or at least abundant elements in the flora. Both species showed on the surface early in March of 1939 and 1940 and were immediately sought out by the deer. Where the water was not much more than a foot in depth the deer waded about in the Oenanthe beds and cropped all vegetative growth down to about two inches beneath the water surface. This heavy browsing of Oenanthe persisted throughout the spring and summer. Flower heads were taken only occasionally and I did not notice the browsing of seed heads. The buttercup was browsed less severely and over a shorter period. I noticed little evidence of its utilization after mid May.

In one part of a small stream an extensive bed of musk *(Mimulus moschatus)* grows in the shallow water of a mud-filled back eddy. The cress-like new growth of these plants in 1940 appeared in early March. This new growth differed from the mature, aerial leaves produced by the plant later in the year in lacking the abundant hairs on leaves and stems. The deer fed in this bed of musk nightly eating not only the tips projecting above the water but the roots and stolons as well. Later in the year, the characteristically hirsute musk plants were browsed very little. In December and January of the mild winter of 1940-41 this aquatic musk bed was still contributing to the food supply of the deer.

On Spider Island and Hunter Island I found deer eating buckbean *(Menyanthes trifoliata)* in considerable quantities. On southern Vancouver Island, however, this plant is rare and on only one or two occasions have I noticed deer browsing upon it.

HERBACEOUS PLANTS

This group of plants is everywhere abundant in the study area during the spring and summer months but contributes little to the diet of the coast deer.

The list of preferred browse species given in Table 18 includes but ten herbaceous plants other than the aquatic species and of these four are wet-ground plants, that flower early. In fact the majority of the highly palatable species belong to two general groups, wet ground species and rock bluff species. These two groups have in common very early spring development.

In the first group belong *Mimulus moschatus, Cardamine breweri, Stachys ciliata,* and *Mentha canadensis.* In the latter group are included *Allium cernuum* and *Camassia quamish.* Of the other species *Hypochaeris radicata* and *Cerastium arvense* are abundant plants on the extensive burned areas, where

they produce the first green growth available in the spring. *Montia parviflora* is a less abundant plant providing similar conditions. All these herbaceous plants are browsed primarily in the spring when the deer eagerly seek for all palatable new growth to relieve the monotony of their winter diet. Hypochaeris however in the Goldstream areas is green all winter and is eaten regularly throughout the year. In the summer the flower heads are extensively browsed.

GRASSES, SEDGES, RUSHES AND FERNS

When living under natural conditions this deer eats very little grass and sedge. Utilization of this food source is confined to the new growth of the plants and in consequence feeding upon grasses, sedges and rushes is restricted to a short period in the spring and another period in the autumn and early winter. During winters such as occurred in 1939-40 and 1940-41 on the Goldstream Summit there was green grass available until mid January and though it was not being extensively eaten a small amount of grazing was noted.

The result of this type of utilization of a grass is marked if corresponding fields grazed by deer and sheep or cattle are compared. Where sheep have pastured the grass will be cut short, with hardly a seed head showing. That grazed by deer, however, appears almost uncropped. The deer avoid the seed heads and in consequence the grasses are able to mature seed. This is most important in the case of annual species that are dependent on the seed crop for their survival.

Only the short new succulent sprouts of sedge are eaten but as the lakes and ponds recede gradually during the summer there is available a fairly steady though very local supply of such new shoots until August at least.

Bracken is in places quite heavily fed upon in the spring. At this time the curled growing tips are nipped off down to the woody part of the stem, six inches or more of each plant may thus be eaten. As the recommended method of killing bracken is the lopping of the stems this type of browsing may have deleterious effects upon the plant if sufficiently intense. In actual practice, however, it seldom involves more than 10 per cent to 20 per cent of the shoots on any area.

The coast deer browses the mature bracken leaves to a small degree during the summer and to a much greater degree in the early autumn. In selecting plants to feed upon there is a marked preference for the tall, succulent plants growing in damp gullies over the shorter, more woody plants of the arid ridges. This was exemplified at Goldstream Lake in October and November 1938 (Fig. 17). Bracken was abundant in all open and semi-open country adjoining the lake but in one area along a small creek entering the north end of the lake it was growing five and six feet in height. Elsewhere on the drier ridges it was unusual to find a plant over two and a half feet and eighteen inches was nearer the average height. Prolonged search failed to find a single

browsed plant on the ridges while the tall bracken along the creek bed had been broken down and almost completely stripped of all petioles so that nothing but the coarse mid ribs and stems remained.

On the Goldstream area two varieties of sword fern occur. *Polystichum munitum* is a tall variety growing for the most part in the timber but still struggling for survival in the newly logged and burned area. On the old burn another race *P. m. imbricans* of more dwarfed habit was of casual occurrence. It was noticed many times that the latter race was selected by the deer in preference to the tall one. In fact *imbricans* was usually moderately browsed during the summer while *munitum* was seldom eaten until winter put a premium upon green vegetation.

FIG. 17. Mature bracken on a damp site, defoliated by deer.

Certain plants are only eaten after they have been killed. In this group the nettle *(Urtica lyallii)* is conspicuous. Deer, even captive deer avid for green vegetation, ignored green nettles. However if the nettles are cut, as soon as wilting sets in the deer eat them with apparent relish. In this case wilting probably affects the stinging bristles also and thus "disarms" the plant.

The false hellebore *(Veratrum viride)* is another plant in this group. I had classed this plant as not eaten by deer until at an altitude of 4,000 feet on Black Mountain, West Vancouver, in October 1932 I found Veratrum being moderately browsed after the first killing frost had turned the leaves brown.

The difficulty of getting reliable identification of fungi restricted the information I was able to assemble on the consumption of these plants by coast deer. Under certain conditions great quantities of mushrooms are eaten.

For instance in November 1930 on Constitution Hill, near Courtenay, B. C., I shot two bucks whose entire stomach contents were dyed purple with the high proportion of a small purple-gilled mushroom. Though specimens were collected I was unable to get them identified.

In October 1931 near Courtenay many instances of deer eating *Clitocybe gigantea* were observed. On several occasions these mushrooms had been dug from

the ground and eaten before they had more than elevated the earth crust over them.

During the late fall and early winter at Goldstream Lake several species of Boletus are abundant. Apparently all these are eaten but *Boletus subaureus* is the only one I was able to establish with certainty. In the early spring on the same area a species of morel was eaten but as it was rare it did not contribute importantly to the food supply of the deer.

Other mushrooms identified as among those eaten by the coast deer are *Tricholoma ? personatum* and *Russula atropurpurea*.

LICHENS, MOSSES, ETC.

A host of species of lichens, mosses and liverworts are available to the deer throughout the year. It is noteworthy that except for certain of the arboreal lichens not one of this large and abundant group of plants enters the diet of the coast deer.

I have taken small fragments of Selaginella and one or two species of moss and two species of liverworts from the stomachs I have examined, but in all cases the deer had been feeding on ground vegetation of a type that suggested the presence of the moss was accidental.

Several species of Cladonia and other rock-loving lichens form extensive mats on many of the rock bluffs so abundant on southern Vancouver Island but only the small, black-spored lichen was eaten with sufficient regularity or in sufficient quantity to class as other than an accidental inclusion in the stomach contents.

Of the three species of arboreal lichens eaten by the coast deer the "Old man's beard moss" *Usnea barbata* is by far the most important.

SUMMARY OF GENERAL BROWSE PREFERENCES

On the study areas of southwest Vancouver Island every wood or herbaceous plant encountered was collected and identified. Notes were kept, over a period of three years, upon the utilization of each plant species by the coast deer as food. In all two hundred and thirty species of plants were so studied. No attempt was made to collect specimens of all lichens, mosses and mushrooms present on the area. In these groups only those contributing to the food supply of the coast deer have been identified.

Table 22 summarizes the general food predilections of this ungulate as revealed by the above study. Of the 223 plant species and subspecies comprising the four major plant categories within which an effort was made to effect a complete inventory, sixty-one are trees and shrubs, one hundred and six herbaceous plants, forty-one grasses, sedges and rushes and fifteen ferns, Equisetums and quillworts. Of the sixty-one trees and shrubs, twenty-six species or forty-three per cent prove to be highly palatable to deer, and an additional seventeen species or 28 per cent moderately palatable. Thus 71 per cent of the trees and shrubs in this region are superior deer food, while only 8 per cent were consistently ignored by deer. Among the one hundred and six herbaceous

plant species, however, quite the reverse is true. Here but 21 per cent of the species are fairly palatable and most of these are available for only a brief period in the spring and early summer. An additional 43 per cent of the herbaceous plants are seldom eaten and 36 per cent were not seen to be utilized at all.

TABLE 22. Relative palatability of various groups of plants exclusive of lichens, mushrooms and mosses.

Floral groups	Highly palatable		Moderately palatable		Low palatability		Not eaten		Total number of species in floral group
	Number of species	Per cent of species in group	Number of species	Per cent of species in group	Number of species	Per cent of species in group	Number of species	Per cent of species in group	
Trees and shrubs	26	43%	17	28%	13	21%	5	8%	61
Herbaceous plants	12	11%	11	10%	45	43%	38	36%	106
Grasses, sedges and rushes	6	15%	7	17%	10	24%	18	44%	41
Ferns, Equisetums and Quillworts	1	7%	4	27%	6	40%	4	26%	15
TOTALS	45		39		74		65		223

The grasses, sedges and rushes display a similar condition, with 32 per cent of the species on the palatable list and 44 per cent on the "not eaten" list. In this case however the difficulty of identifying many grasses until late in the season, long after the period of grazing by deer, makes it probable that some of the species listed by me as "not eaten" on further study will be found to be taken occasionally.

It must be evident from the above that the coast deer is a browsing animal and that it prefers the foliage of woody plants to that of herbaceous plants.

CONCLUSIONS

1. Of the three wet ground associes and five dry ground associes examined on southern Vancouver Island the deciduous pioneer forest (Arbutus-Spiraea-Gaultheria associes) and the coniferous pioneer forest (Pseudotsuga-Gaultheria associes) are the two most desirable deer habitats. In these the dominant and important subdominant plants are at the same time desirable food species.

2. Where no domestic livestock are present these two communities can, under optimum conditions, support deer populations of from 20 to 30 per square mile. Forty deer per square mile produce an overgrazed condition.

3. The new burn community (Epilobium-Senecio associes) and coniferous subclimax forest (Pseudotsuga consocies) both extensive in area can each support small deer populations.

4. The other four, viz., mud-flat community (Juncus-Carex-Isoetes associes), the sedge meadow community (Carex-Oenanthe associes), alder community (Alnus-Salix associes), and the rock-bluff community (Polytrichum-Aira associes) are of value to deer for the most part as supplemental seasonal foraging and bedding grounds.

5. Deer avoid the seed heads of grasses and sedges and consequently damage the range grasses less than do ungulates that remove the seed heads.

6. The coast deer on Vancouver Island does not normally feed in water deeper than 8 or 10 inches. It avoids dense thickets when feeding, prefers to have its front feet higher than its hind feet and browses more heavily on side hill areas than on flat areas where both are available.

7. Thorns on plants have a real protective value against deer browsing.

8. Examination of food plants in the field and in deer stomachs reveals the coast deer as a browser. Roughly 67 per cent of the annual diet consisted of twigs and leaves of trees and shrubs (24 per cent conifer browse and 43 per cent deciduous browse). A further 15 per cent of the annual diet was supplied by arboreal lichens, chiefly Usnea, 11 per cent by herbaceous plants, 5 per cent by mushrooms, and 2 per cent by grasses, sedges and miscellaneous plants.

9. The most important browse species on the Goldstream area were found to be Douglas fir, salal, Old man's beard lichen, alder, willow, bracken, thimbleberry, marestail and cedar in that order. In deciduous pioneer second growth, madrone, spiraea and dogwood are included in this list.

10. Browsing upon seedling and second growth Douglas fir is often severe, on inferior forest types it may approach 100 per cent.

11. The intensity of browse effort on Douglas fir was found to be directly associated with the density of the fir stand. At densities in excess of 12 per milacre the percentage of utilization becomes significantly reduced.

12. Where the seashore is at hand various seaweeds are added to the diet. Wood ash and charcoal are frequently eaten. Skeletons and shed antlers are quickly consumed. In coastal British Columbia the coast deer does not use licks.

13. Of 230 species of plants studied with regard to their status as deer food, 61 were trees and shrubs; 71 per cent of these were found to be highly palatable or moderately palatable to deer, only 8 per cent were not browsed. Only 22 per cent of 106 herbaceous species fell in the preferred list. Similarly only 32 per cent of the grasses, sedges and miscellaneous plant species appear to be palatable.

14. Deer do not browse western hemlock. Thus where deer are abundant, artificial reforestation might well utilize this species in preference to Douglas fir, where site conditions are suitable.

15. Salal *(Gaultheria shallon)* growing in the open under semi-arid conditions and of resultant dwarf habit was browsed in preference to the same plant growing in shaded and moist localities.

16. The seeds of a number of berry bearing plants pass through the ungulate digestive tract undamaged. Seeds of Amelanchier, Rosa and Gaultheria germinated after passage. Thus the deer may serve to distribute such forms.

17. Deer infrequently kill shrubs and trees. However, such preferred species as the red huckleberry *(Vaccinium parvifolium)* and flowering currant *(Ribes sanguinea)* under pressure of 20 deer per square mile seldom produce fruit.

MANAGEMENT SUGGESTIONS

In British Columbia the coast deer is primarily an inhabitant of pioneer forest communities. Removal of either a climax conifer forest or a subclimax Douglas fir forest improves the environment for this deer. Thus logging is directly responsible for producing improved conditions for deer.

Where fire is the deforesting agent or succeeds the deforestation, the deer carrying capacity is not immediately increased but improves gradually to an optimum in approximately 10 to 15 years.

Optimum conditions for coast deer occur where a rolling or broken terrain supports a diversified cover in which young second growth forests predominate but where blocks of older timber are interspersed. This suggests that a logging program under which clean logging of blocks of land of approximately 1 square mile in area is practiced, with unlogged blocks left between logged areas, can be expected to produce near optimum conditions for coast deer.

Certain Vancouver Island logging operators are already experimenting with such a technique because it offers advantages from the standpoint of the logger and silviculturist.

Where habitat improvement is the aim, the highly palatable forage species should be encouraged (Table 12). For winter food one of the most important of these is the Douglas fir.

Where it is desired to establish escape coverts for upland game birds or lesser wildlife in areas supporting a heavy deer population, such spiny shrubs as the roses and gooseberries, or unpalatable species as manzanita, evergreen huckleberry or broom should be used.

When conifer plantings for ornamental or other purposes are desired on areas where they will be subject to deer browsing, jack pine, western white pine, western hemlock, Rocky mountain juniper and Oregon yew will prove of minimum attraction to the deer.

It has been found that deer can occasion serious damage to second growth Douglas fir regenerating on deforested areas. The influence of deer on regenerating fir depends not alone on the density of deer but to a great extent also on the density of second growth trees (p. 129).

Current reforestation practice with Douglas fir seedlings planted at approximately 1,200 per acre provides conditions under which maximum deer damage can be expected.

Where seeding, natural or artificial, gave rise to seedlings in excess of 12,000 per acre, deer damage was found to be unimportant.

If reforestation of a good site takes place within a year or two following the logging and burning of

a mature fir forest, and on an area of sufficient size to be beyond the normal cruising radius of a deer from good cover, the trees are usually beyond the reach of deer before the population reaches destructive levels. On a poor site, however, such may not be the case.

Cedar was the only winter browse species found that had a palatability as great as that of Douglas fir. However, the ecological requirements, alone, of this tree render it of little use as a buffer.

Two types of Douglas fir were noted among natural regeneration on southern Vancouver Island, normal trees and yellow trees. The latter had a significantly lower palatability than the former (p. 123), and the determination of the cause behind the appearance of these yellow trees or the reason for their reduced palatability might point to a means of reducing deer damage on Douglas fir plantations.

Much of the logging industry of the northwest has been built around the Douglas fir. However, as the stands of this species become depleted, the western hemlock is coming into increasing favor as a timber tree. The hemlock is not eaten by deer and offers itself as a useful species for the reforestation of suitable sites where deer damage to firs might render the use of that species impracticable. Such conditions frequently occur on old logging operations where natural regeneration of conifers has not taken place and which now support a heavy growth of deciduous trees and shrubs.

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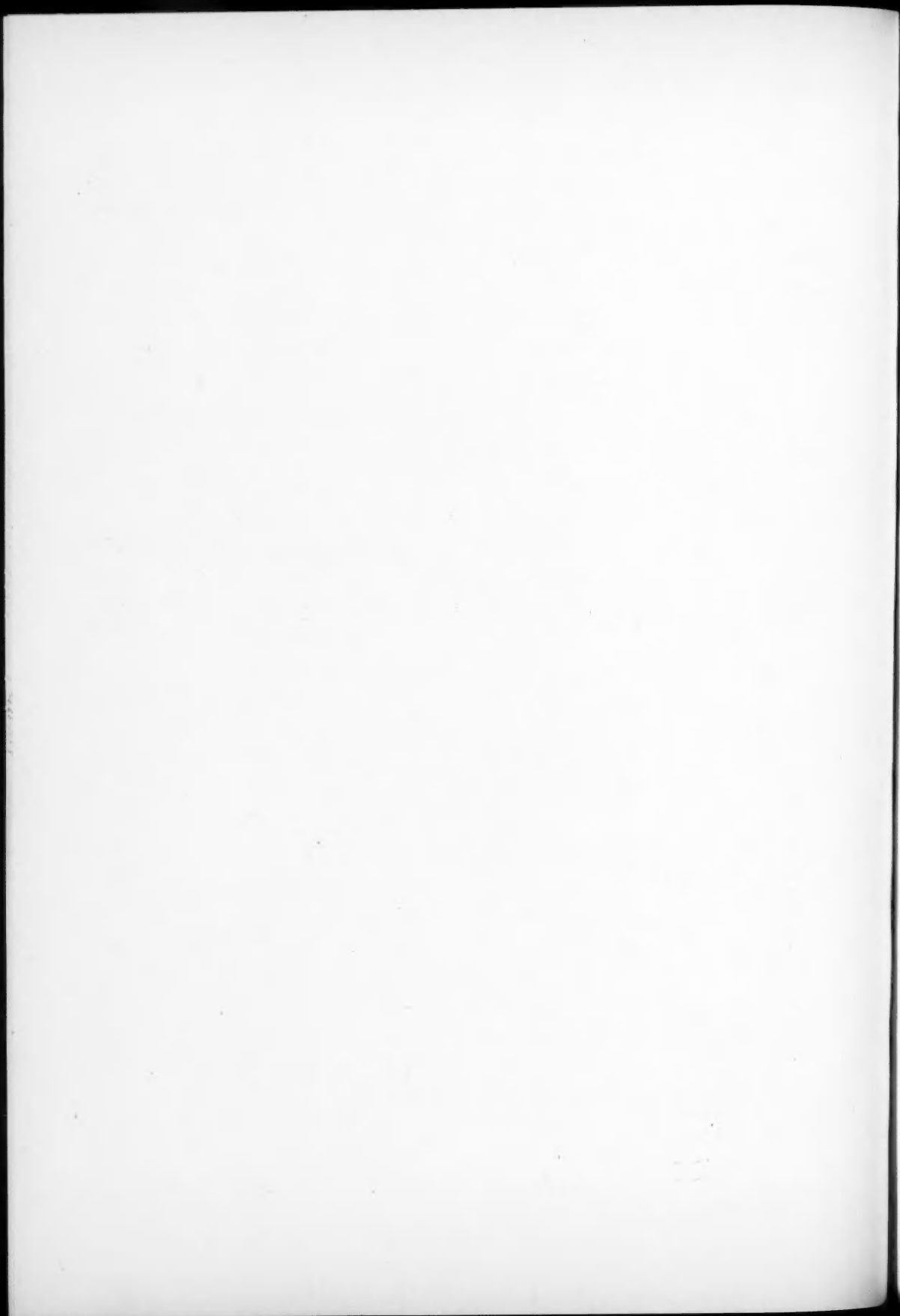
ECOLOGICAL STUDIES OF SESSILE ROTATORIA

PART II

Dynamics of Populations and Social Structures

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ECOLOGICAL STUDIES OF SESSILE ROTATORIA

PART II

DYNAMICS OF POPULATIONS AND SOCIAL STRUCTURES

INTRODUCTION

The present paper discusses three related topics which concern certain natural populations of sessile Rotatoria. These are the form and dynamics of populations, and the effects of aggregation in one species. Form, as used here, means the arrangement and distribution of individuals on substrates, while dynamics is used to refer to all rates of change in characteristics of populations. These rates have to do with seasonal differences in numbers, reproduction, growth, death and spatial translocation of populations as a whole. First, general observations are discussed. Then follows an analysis of as many aspects of population physiology as can be convincingly obtained from the data.

A brief discussion of general techniques was given in Part I (Edmondson 1944). Special techniques are discussed in connection with the presentation of data in each section here. Acknowledgment has already been made in Part I of the help received in this work. The author wishes to reiterate his appreciation for that help.

The populations most studied were those found living on *Utricularia vulgaris americana* in a small pond in the Yale Bird Preserve, Woodbridge, Connecticut. While twelve species of sessile Rotatoria have been found in the pond, only four occurred abundantly enough to be studied extensively. These are *Floscularia conifera* (Hudson 1886), *Collotheca gracilipes* Edmondson (1940), *Beauchampia crucigera* (Dutrochet 1812) and *Ptygura longicornis bispicata* Edmondson (1944). The pond was formed in 1916 by damming a small stream which originates from springs near the top of a hill. The general shape is that of a segment of a circle about 300 feet long and about 40 feet wide. The depth varies in most parts from 2 to 3 feet, but near the dam reaches 10 feet. There is a small rustic bridge at the widest part, and this furnishes a convenient platform for working. The most abundant plant is Chara which forms a carpet of rather uniform density in all shallower parts of the pond. *Utricularia vulgaris americana* (to be referred to henceforth simply by the generic name) grows evenly distributed throughout the pond, plants lying on or within the Chara carpet. *Potamogeton pusillus* and *Typha latifolia* grow around the edges. The water has a mean pH of 7.6 and a mean bicarbonate concentration of 59.2 mgm./1. The color is a mild brown, about 30 on the U. S. G. S. scale. The fauna was studied from a number of aspects during the summers of 1940 and 1941. Late in September, 1940, the pond was partly drained so that a stronger dam could be built. Since this no doubt affected the course of events in 1941, most attention will be given to observations made in 1940.

SEASONAL OCCURRENCE

METHODS

Determination of population size. In determining the size of populations, usually the number of individuals on an entire Utricularia plant was counted. The leaves were cut from the plant one at a time, starting at the growing tip. Each leaf was carefully examined, cut into small pieces if necessary, and the number of each species of rotifer recorded. The stem was also examined in sections. For the sake of uniformity, however, all data given refer to the leaf fauna unless specifically excepted. When populations were very large, the time-consuming nature of the counts made it impossible to examine all leaves of large plants, but an effort was always made to extend the count to the end of the plant, and none of the counts recorded here stops very far short of the end.

Determination of substrate area. To measure the area of Utricularia plants, a drawing of every tenth leaf was made with a projecting microscope at six diameters magnification, and the area of the drawing measured with a planimeter. All leaves were put on a 3″ x 2″ glass slide, flooded with water, and covered with a 2″ x 1.5″ slide. It was usually necessary to cut the leaves into sections. The Utricularia leaf, as well as that of Myriophyllum and a number of other plants, can be regarded as a series of cylinders joined together at the ends in branching form (Fig. 1). A little reflection shows that the lateral area of a cylinder with circular cross section is π times the area of a longitudinal section. Therefore, planimeter readings were multiplied by π and divided by the square of the magnification to give the actual area. This gives but an approximation since there are irregularities, especially at the points of branching, but it serves well enough as all the leaves are of similar form. The bladders were not flat (factor of 2), cylinders (factor of π), nor spheres (factor of 4), but it was found by studying the true area obtained by squeezing them flat, that a factor of π gave a very good approximation under the conditions of drawing. Sometimes Utricularia leaves were noticeably flattened, especially near the tips. It was then necessary to introduce a factor to allow for the flattening. The factor used was the ratio of the perimeter of an ellipse to that of a circumscribed circle, the constants of the ellipse being determined by

measuring the short and long diameters of leaves at several places and taking the mean ratio.

Thus, knowing the mean area of the leaves and the number examined, it was possible to estimate the area of the plant. This method has the advantage of giving the area of plants with divided leaves so that the abundance of rotifers can be expressed in a reasonable way, as number on unit area. It has the distinct disadvantages of taking much time, being tedious, and being subject to unavoidable errors of tracing, measurement and calculation, which reduce its accuracy.

Other plants can be measured more simply. Cylindrical hard leaves, such as those of Chara, can be cut into their component sections and these measured with rule and micrometer eyepiece. Leaves with straight, parallel edges, as some species of Potamogeton, were measured in length and width, and area calculated making allowance for rounded ends. Floating leaves such as those of lily pads can be traced rapidly on paper and the area measured with a planimeter. The area of large, cylindrical stems can be calculated from direct measurements. Studies based on plants with such stems have been made previously; e.g., Miller (1934), Meschkat (1934) and Young (1942).

Volumetric Expression of Population Size. The abundance of rotifer populations attached to plants of the same general structure as Myriophyllum or Utricularia can be expressed as number in unit volume by measuring the volume of water closely associated with the plant. This was done by measuring the length of leaves at regular intervals along the stem. The volume of water was then calculated as a series of cylinders, each of which was determined by the mean length of two leaves as radius and the distance between as length. This method of expression is easy to calculate, but since the area of plant contained in unit volume is rather variable, it is of less significance than a direct areal measure.

RESULTS

Seasonal distribution of all species in many habitats did not form a large part of the present work, and only a general statement can be made. Collections were taken during all months of the year from many ponds and lakes. It is quite evident from them that few sessile rotifers occur in cold water, unlike many free-swimming species. The author has never found any sessile species in quantity at temperatures lower than 15° C., and all occurrences of huge populations have been in water warmer than 20°. It was found in some rough, preliminary laboratory experiments that growth of adults and hatching of eggs of *Floscularia conifera* stops at about 10°. It is doubtful, however, that temperature is the only factor governing the appearance or disappearance of species in habitats.

During the summer of 1940, fluctuations in number of individuals of species living on Utricularia in the Bird Preserve Pond were studied. Table 1 shows the data for the three most abundant species, and the same data are shown graphically in Figure 2. *Floscularia conifera* multiplied rapidly between the first week of June and the middle of July, reaching a maximum on July 13. The number fell rapidly after that date, and by September 10, the species had disappeared from the pond. The maximum population observed was represented by 2,480 individuals on one Utricularia plant. The volumetric abundance of the species is shown in the lower part of Table 1. The figures are not strictly proportional to the areal figures because of the variation in the amount of plant surface in each unit volume.

Collotheca gracilipes varied irregularly in numbers during the season, but was never as abundant as the maximum of *Floscularia conifera*. The concentra-
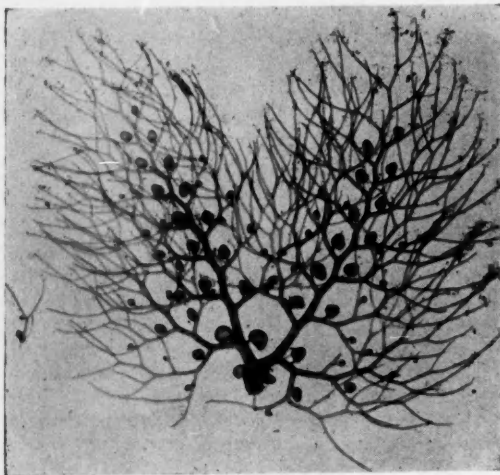
FIG. 1. Leaf number 7 of a *Utricularia vulgaris americana* collected at Woodbridge Skating Rink, August 26, 1941; × 3. A great many *Collotheca gracilipes* may be seen as specks near the tips of the divisions of the leaf.

Table 1. Abundance of three species of sessile Rotatoria in Bird Preserve Pond. Above is shown the mean number of individuals per square centimeter of Utricularia leaf, below the mean number per liter of water calculated in the manner described in the text. Data for *Collotheca gracilipes* are based on the area and volume of the first twenty leaves, while others are based on all leaves examined, shown in Figures 4 and 6.

Date, 1940		*Floscularia conifera*	*Collotheca gracilipes*	*Beauchampia crucigera*
June	7....	0.9	0.2	0.3
June	27....	9.2	1.6	3.1
July	13....	12.6	0.5	1.8
July	25....	5.0	1.3	0.2
August	7....	4.9	0.2	0.0
September	10....	0.0	1.5	0.0
June	7....	198	29	73
June	27....	1235	220	431
July	13....	3346	69	486
July	25....	1249	271	42
August	7....	1606	57	0
September	10....	0	528	0
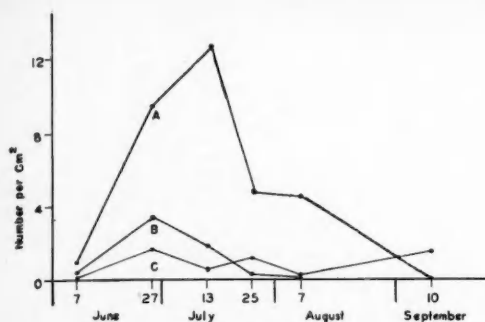
FIG. 2. Abundance of three species of sessile Rotatoria in Bird Preserve Pond during 1940, expressed as number per square centimeter of leaf surface of *Utricularia vulgaris americana*. A, *Floscularia conifera;* B, *Beauchampia crucigera;* C, *Collotheca gracilipes*.

tions given for Collotheca in Table 1 and Figure 2 were calculated on the basis of the first twenty leaves of each plant, because this rotifer occurred in greatest numbers on that part of the plant and was rarely found farther back. Since only one plant was examined quantitatively on each date, it may be that the apparent irregularity of seasonal distribution is a result of irregular distribution in the pond, although plants were always taken as nearly as possible in the same place. A general examination showed Floscularia to be more homogeneously distributed through the pond than was Collotheca. The data on the former undoubtedly reveal real fluctuations in population, while the latter may be partly distorted. *Beauchampia crucigera* reached a maximum on June 27, earlier than *Floscularia conifera,* and died out much sooner.

In 1941 fluctuations were not followed so closely. *Floscularia conifera* remained in fairly low numbers until the end of July (Table 2, *total* column). During this time the water of the pond was much darker than any time in 1940, and the surface was largely

TABLE 2. Distribution of *Floscularia conifera* on *Utricularia vulgaris americana* in the Bird Preserve Pond. Each figure shows the number of rotifers on groups of five leaves. Each group is indicated in order from the growing tip of the plant by a Roman numeral and a letter.

Section	Ia	Ib	IIa	IIb	IIIa	IIIb	IVa	IVb	Total
Date—1940									
June 7...	1	3	6	3	10	14	25	14	76
June 27...	45	76	184	224	548	151	..	..	1228
July 13...	5	31	59	147	495	671	525	493	2426
July 25...	12	44	50	80	115	285	151	..	733
August 7...	0	2	13	90	184	198	351	..	838
1941									
June 8...	1	1	1	1	0	..	..	..	4
June 23...	5	14	29	28	74	177	..	..	327
July 5...	0	19	43	60	..	..	..	..	122
July 21...	12	27	39	51	28	18	..	..	175
August 18...	12	50	126	287	492	313	..	..	1280

covered by floating mats of Mougeotia which shaded the bottom and which remained until the middle of July. This and associated conditions were perhaps major factors in keeping the fauna at low numbers. Utricularia did not start growing well until the middle of June, almost three weeks later than in the previous year. By the middle of August a fairly large population of Floscularia had developed, which persisted into September, but at no time did the numbers approach those of the 1940 maximum.

Collotheca gracilipes appeared irregularly and in small numbers during most of 1941; however, on May 6, a very small Utricularia plant, evidently just starting to grow, was found floating near the surface of the water. On this plant were many animals, more than 160 on 5 leaves. Most were young, and the adults were reproducing rapidly, some having as many as six eggs in the tube. It was more than a month later that Utricularia started to grow in any abundance, only isolated plants being found occasionally until then. Apparently resting eggs left from 1940 had begun to hatch at the usual time in 1941, but before there was sufficient substrate available. It is known that *Collotheca gracilipes* is practically restricted to Utricularia (Part I). Very likely by the time Utricularia was growing well, most of the resting eggs had hatched and many of the resulting larvae had either died or formed abortive populations, only the few late hatching ones having been able to maintain themselves. This suggests that the seasonal growth of plants has an effect on species which show substrate preference, and dislocation of the normal seasonal development of the flora can have a profound effect on the fauna. It is probable that resting eggs produced during one season hatch during a considerable period of time the next year so that there are usually larvae present when the plants appear.

Late in August, 1941, a burst of reproduction occurred in Woodbridge Skating Rink Pond. Here the young leaves of many Utricularia plants looked filmy to the naked eye and were literally covered with the rotifers. It was estimated that the concentration was equivalent to at least 25,000 animals per liter of water. Figure 1 shows a leaf taken from this locality about two weeks before the maximum, but fair numbers of animals can be seen nevertheless, especially at the tips of the divisions of the leaf.

FORM OF POPULATIONS

In making counts for the study of seasonal distribution in Bird Preserve Pond, it was noticed that animals were not evenly distributed from one end of the plant to the other, but that there was a maximum concentration at one particular region. Such a distribution might be expected, since leaves near the growing tip are younger and would have had less time to acquire a population. The species, however, varied from this distribution in different ways, so that factors other than age of leaves are involved.

A note on Utricularia is necessary at this point. Figures of the entire plant can be found in works by

Fassett (1940) and Martin & Uhler (1939). It is a small herb of the family Lentibulariaceae, commonly called bladderwort. Each plant consists of a long, cylindrical, slender stem about 2 to 3 millimeters in diameter with a series of alternate, dissected leaves. Each leaf consists of two leaflets so deeply separated as to appear as two leaves. The form of a typical young leaf is shown in Figure 1. At one end of the stem is a region of active meristem, the growing bud from which new leaves are constantly being formed. There are no roots. In subsequent discussion, the growing tip will be called the distal end, while the other end of the plant will be called the proximal end. The leaves at the proximal end are older than those at the distal, and any one leaf is older than the one immediately in front of it. The proximal end of the plant dies and disintegrates as the distal end grows; the rates of the two processes and age of the plant determine its length at any moment. Lateral buds are often formed, giving rise eventually to separate plants when the tissues of the joint disintegrate. As the leaves grow, small vesicles appear at definite places which eventually grow to form the hollow bladders for which the plant is named. Each has an opening with a valve which permits entry but not exit to small animals, and the plant is famous for its ability to trap great numbers of them. In time the bladders drop off, so that the moribund and decaying leaves at the proximal of the plant have no bladders.

Floscularia conifera

Floscularia conifera was the most abundant species and the one on which most data were obtained. Figure 3 shows a typical distribution pattern, giving the number of individuals attached to each leaf on a single plant. While there is considerable irregularity, the trend is from few animals at the distal end to a maximum, and a reduction in numbers toward the proximal. This is shown more clearly in Figures 4 and 5 where the leaves are taken in groups of five, starting at the distal end. The data on which the figures are based are given in Table 2. Although the size of the leaves varies along the plant, this difference in number is also a difference in concentration. This may be seen in a collection taken June 27, 1940, for example. There the numbers of animals counted on the 1st, 10th, 20th and 30th leaves were, respectively 4, 18, 33 and 1, while the concentration obtained by dividing these numbers by the areas of the leaves were, respectively, 3.8, 6.6, 13.5, and 0.7 per cm². This fact suggests that Floscularia larvae are sensitive to differences in the substrate, and tend to some extent to avoid the oldest, disintegrating leaves in favor of those that are younger and firmer. Experimental indication of such preference was given in Part I (Edmondson 1944), and statistical evidence is to be presented later.

Floscularia occurred also on the stems, but infrequently. The concentration of the species on stems on the first three dates in Table 1 were 0.5, 1.9 and 0.5 per square centimeter as contrasted to the much higher concentration on leaves.
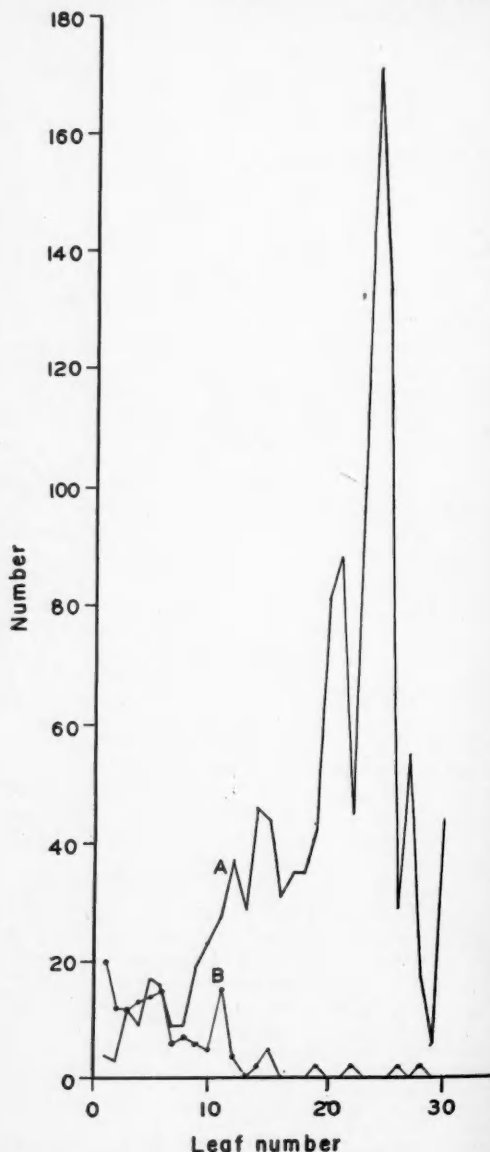
FIG. 3. Numbers of *Floscularia conifera* (A) and *Collotheca gracilipes* (B) on each leaf of a *Utricularia vulgaris americana* collected at Bird Preserve Pond, June 27, 1940.

Beauchampia crucigera

Beauchampia crucigera, when fairly abundant, showed a distribution pattern similar to that of Floscularia (Fig. 16). Generally, however, the species was so scarce that the distribution was irregular.

Ptygura longicornis bispicata

Ptygura longicornis bispicata was usually too scarce to show a definite form of distribution along the
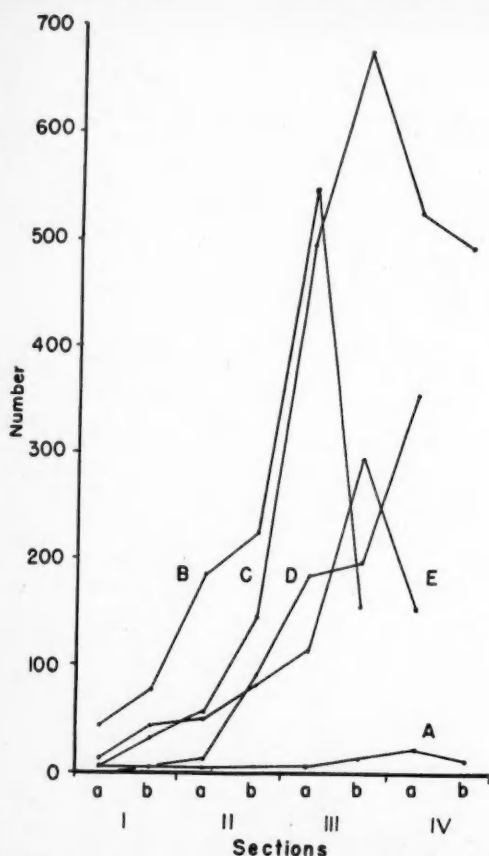
FIG. 4. Distribution of *Floscularia conifera* along the axis of a *Utricularia vulgaris americana* on five dates in 1940, Bird Preserve Pond. Each point represents the total number of animals on a group of five leaves. The groups are designated in order by a Roman numeral and a letter. A, June 7; B, June 27; C, July 13; D, July 25; E, August 7.

plant, but when relatively abundant, formed a definite maximum well toward the proximal end (Fig. 17).

Collotheca gracilipes

Collotheca gracilipes always showed a remarkable distribution pattern quite different from the three species described so far. This is shown in Fig. 6 and especially in Fig. 3 where it is compared with *Floscularia conifera*. There was usually an abrupt rise to a maximum, often very large, and a less abrupt decrease to zero. In only one case was the maximum farther back than the tenth leaf. The oldest leaf ever to have the species in a regular count was number 32, but the numbers of Collotheca were usually inconsiderable behind leaf 20. This distribution is apparently the result of a very strong preference on the part of the larvae for young leaves, demonstrated experimentally in Part I, which seems
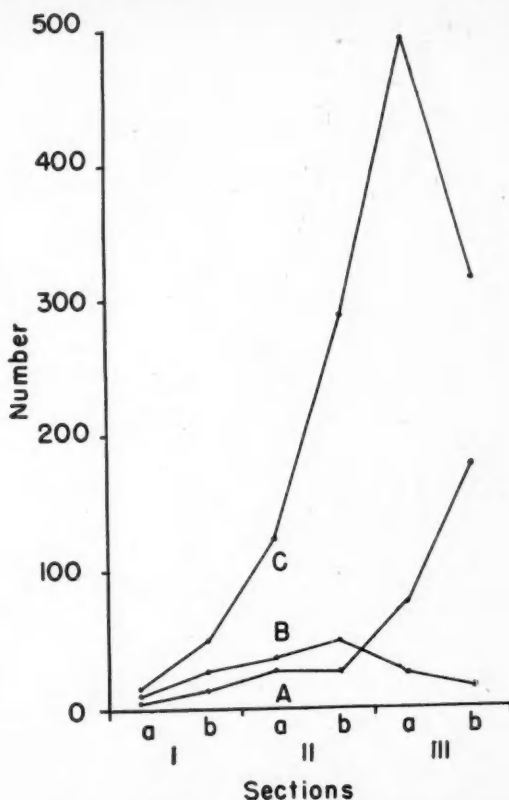
FIG. 5 Distribution of *Floscularia conifera* along the axis of a *Utricularia vulgaris americana* on three dates in 1941, Bird Preserve Pond. A, June 25; B, July 21; C, August 18. Other explanation as in Fig. 4.

to be based on chemical differences between leaves of different age. There was a distinct differential age distribution of animals along the plant, with very young animals on the youngest leaves and sometimes the bud; older animals occur only farther back. This may be shown by listing the number of young and of old animals on the first fifteen leaves of a plant. The leaves were grouped by fives.

Leaves	Number of young animals	Number of old animals
1– 5	13	5
6–10	19	62
11–15	5	10

Young animals can be distinguished by relatively short foot, thick pedal hypodermis and small corona, while older individuals have a long, slender foot, large, bowl-shaped corona and a thin hypodermis in the foot. Adults usually have eggs in the tube.

The very large population in Woodbridge Skating Rink, previously mentioned, showed this type of distribution very well. The bud of the Utricularia had a fair number of very young animals. The first leaf of one plant had about 300, the second well over 1,200 individuals, and the leaves behind this had too many
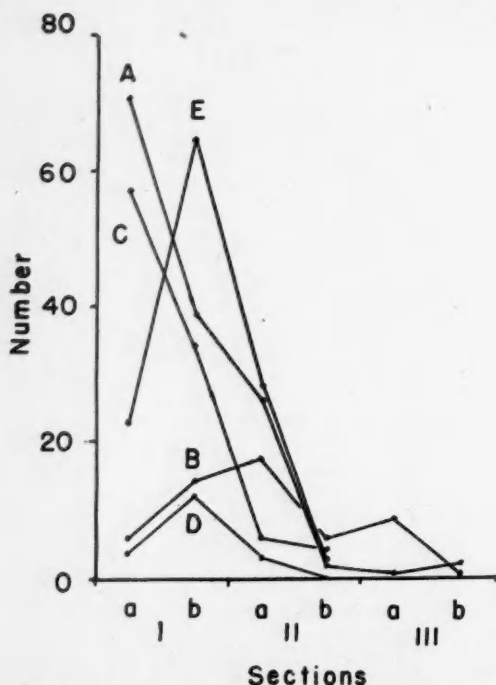
FIG. 6. Distribution of *Collotheca gracilipes* along the axis of a *Utricularia vulgaris americana* on five dates in 1940, Bird Preserve Pond. Other explanation as in Fig. 4.

TABLE 3. Distribution of *Collotheca gracilipes* on Utricularia in the Bird Preserve Pond, 1940. Explanation as in Table 2.

Section		Ia	Ib	IIa	IIb	IIIa	IIIb	IVa	IVb	Total
Date										
June	7	0	1	2	1	0	0	1	0	5
June	27	71	39	26	2	1	2	0	0	141
July	13	6	14	17	6	9	1	0	0	53
July	25	57	34	6	4	0	0	0	0	101
August	7	4	12	3	0	0	0	0	..	19
September	10	25	65	28	3	0	0	..	..	121

to count. The age distribution was very evident to the eye, for the animals on the bud were very small, while egg-bearing animals did not occur until several leaves away from the bud. There were few animals on the twentieth leaf.

To summarize, in the four species studied, two different types of distribution occur. *Floscularia conifera, Beauchampia crucigera* and *Ptygura longicornis bispicata* have the maximum number some distance from the growing tip of the plant. This preliminary examination of the situation suggests that young leaves bear few animals because there has not been time since formation for a large number of larvae to attach with the existing rate of migration. The falling off of numbers toward the priximal end suggests simply that rotifers do not attach freely to moribund leaves which are often covered with bacteria and algae, and thus offer an insecure attachment. *Collotheca gracilipes,* on the other hand, has its maximum numbers quite near the distal end of the plant. This evidently results from the strongly negative reaction to older leaves, and perhaps a corresponding positive reaction to younger individuals. The difference between the distributions is simply in the location of the maximum and the shape of the graph representing the distribution of the animals. Both distributions however have definite maxima except in small or undeveloped populations (Fig. 4, curve A).

DYNAMICS OF POPULATIONS

METHODS

Determination of Rates of Reproduction, Growth and Death in Natural Populations. Some of the species encountered in this study possess characteristics which permit determination in natural habitats of rates of reproduction, growth, death, and other activities, with only slight disturbance of existing conditions. *Floscularia conifera* builds a cylindrical tube in which it lives (Fig. 7). The process of tube
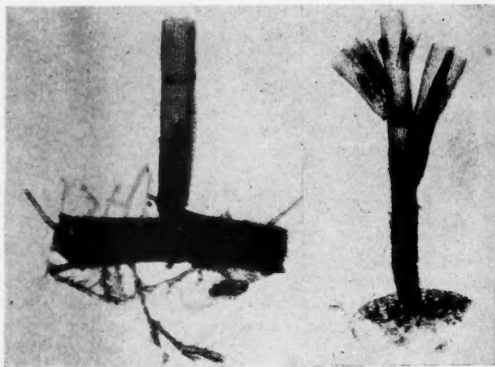
FIG. 7. Photographs of tubes of *Floscularia conifera* from Experiment 1. Left, a solitary animal showing clearly the carmine mark, × 33. Right, a colony of eight individuals, with carmine marks obscure, × 25. The animals are contracted into the bottoms of the tubes.

building in this genus was first described by Leeuwenhoek in 1703 (Dobell 1932, Hudson & Gosse 1886) and has received considerable attention from later investigators; e.g., Gosse (1849), Hudson & Gosse (1886). The young animal, just settled, secretes around itself a rough tube of gelatinous material which forms the base of the main tube. The animal has a conical, ciliated depression on the ventral side just posterior to the mouth (Fig. 8). A large gland secretes a gelatinous material into this cup. Small particles of solid material are collected from the water by ciliary currents set up by the corona; these are mixed with the glandular secretion in the cup until it is filled by a pellet composed of particulate matter cemented together by the rather firm gelat-
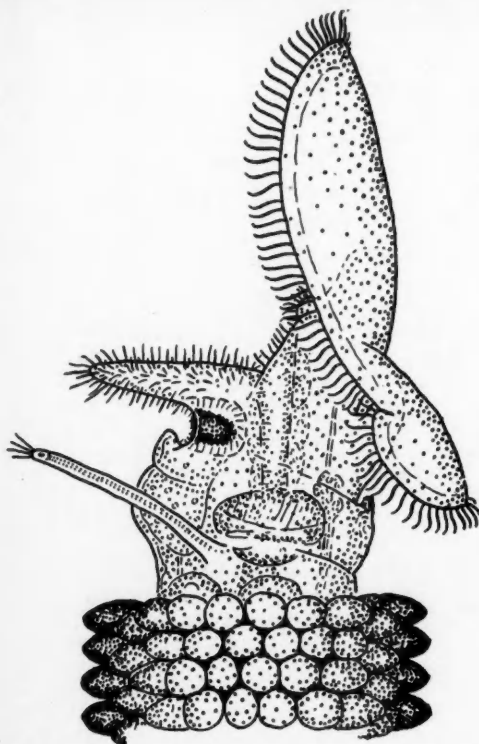
FIG. 8. Drawing of anterior end of *Floscularia coni-fera* in lateral view. The formative pellet shows as a dark object below the ciliated chin.

inous secretion. As the pellet is formed, it is rotated by the cilia in the cup, giving it a smooth and symmetrical shape something like that of a modern pistol bullet. Then, by appropriate movements of head and body, the pellet is pushed on to the top of the tube, so placed that the long axis of the pellet lies along a radius of the tube, the more pointed end outside. This is repeated at frequent intervals, and as the animal grows a tube is built up around it, the top always being at a rather definite level with reference to the pellet-making cup so that growth of the animal is matched by equal growth of the tube.

Now it has long been known that powdered carmine, when added to water containing Floscularia, is incorporated into the pellet, forming bright red tubes. This fact is the basis of the present method. If the tubes of all animals alive at a given moment in a definite part of a pond can be marked with carmine, it should be possible to determine at a later moment how many new animals have settled down during the interval, for they will have no marks. Also, since the growth of the tube is a close measure of the growth of the animal making it, the amount of growth during the interval can be determined for each animal, and a mean growth rate for the population calculated. Furthermore, since the animals disintegrate very soon after death, and since they

must be alive to incorporate carmine into the tubes, it is possible to determine the death rate simply by counting all dead animals which have a carmine mark on their tubes. In determining the reproductive rate, it is necessary to assume that there is no significant amount of immigration or emigration of larvae from the marked region, or if there is, that the two processes are equal. Unfortunately there is yet no direct measure of larval mortality, so what is spoken of as reproductive rate is only the effective rate or rate of settling. This is to be understood in all references to reproductive rate in these experiments unless otherwise stated. A method of estimating the actual reproductive rate will be discussed further on.

The technique used was simple. First a suitable Utricularia plant was selected near the bridge at Bird Preserve Pond. A quantity, usually three or four grams, of carmine was shaken up in about three liters of pond water and poured through a long glass tube with a funnel at the upper end. The tube was manipulated so as to make a large cloud of carmine in the water immediately over and among the leaves of the selected plant. Since carmine settles out fairly soon, it was necessary to add it rather slowly so that all animals had an opportunity to make several pellets; usually twenty minutes was taken for marking. The settling out of the carmine is of great advantage since the animals are not subjected to its presence for very long. Twenty-four hours after marking, the plant was lifted from the water into a jar of pond water and immediately fixed with formalin. In the laboratory, the leaves of the plant were carefully dissected under a binocular dissecting microscope and all Floscularia tubes retained for counting and measuring. Measurements were made to the nearest 10μ.

The method was elaborated by marking the animals three times at intervals of twenty-four hours and then collecting. If tubes are to be marked more than once it is best to use materials of different color. It was found that decolorizing charcoal, finely powdered, was even more satisfactory than carmine since it was utilized much more readily and made a more prominent mark. Moreover, it has the advantage of sticking to the tops of the tubes of *Beauchampia crucigera* and *Ptygura longicornis bispicata* which carmine does only occasionally.

There were at least three possibly disturbing factors in the experiments. First, the currents formed in the pond when the carmine was introduced perhaps washed some of the free-swimming larvae out of the experimental area. Second, it was possible that the presence of carmine in the water and gut would either stimulate or depress growth and reproduction. Third, if the tubes swelled or shrank under the influence of formalin, growth rate measurements would need correction. Since addition of carmine took such a small part of the experimental period and anyway probably would wash as many larvae back into the area as were washed out, the first factor may be safely neglected. Both of the other possibilities were studied.

In order to test the effect of carmine on rate of growth, many Floscu'aria were put into two Syracuse

dishes filled with pond water. To one of these was added a heavy suspension of carmine, and the two dishes were kept under identical conditions for twenty-four hours. Because the animals were near the bottom of the dish, those with carmine made red pellets during the entire time. At the end of the day, the length of the red band was measured. The lengths of the unmarked individuals were measured at the beginning and end of the period. The mean increment of length in the two dishes was not significantly different. Therefore, it must be considered that the use of carmine has no effect on the growth rate, especially when it is remembered that the animals in the pond are not subjected to the presence of carmine for more than a half hour as compared to twenty-four hours in the Syracuse dishes. The effect of charcoal on growth rate was determined by growing numbers of animals in two dishes as before, but to one was added carmine, to the other charcoal. The growth rate for twenty-four hours was about 20% less in the dish with charcoal than in the other, but this is probably of no consequence in the pond experiments since the animals were exposed to carbon for a much shorter time and the concentration of charcoal was very much lower. No conclusive data regarding the effect of carmine and carbon on reproductive rate were obtained, since it is practically impossible to select two manageable groups of animals in the same reproductive state. It seems likely, however, that if the growth rate is unaffected by filling the gut with non-nutritive material, the reproductive rate over so short a period would also be unaffected.

The effect of formalin on the length of the tubes was examined by measuring a group of one hundred tubes immediately after collection and after fixation in formalin for about a month The very small difference in mean length was insignificant.

From these considerations it is judged that the use of carmine and carbon in the experiments gives reliable information about the apparent reproductive, death and growth rates of the three species. Carbon, because of its properties as an absorbent, should be of value in studying other species which make their tubes in the same way as those studied by the writer. It does not seem to stick to tubes of *Collotheca gracilipes*, which are made of a transparent, clear material, and it may be expected that species which make tubes of the same kind cannot be studied with the carbon method. It is hoped that materials will be found which will stick to these tubes without disturb'ng the animals. Other species which probably can be marked with carbon are *Floscularia pedunculata, F. ringens, Limnias myriophylli, Ptygura barbata, P. brevis, P. crystallina, P. longicornis, P. pilula, P. beauchampi* and perhaps *P. linguata* and *P. tacita*. The two species of Floscularia listed make the'r tubes in the same way as *F. conifera*. *Floscularia janus* makes its tube from its own fecal matter, but does not seem to swallow carmine as does *F. conifera*, and it may be that *P. pilula* which makes its tube of fecal matter also cannot be marked. Carbon has not yet been tried on either. The method

described here can certainly be extended to other groups of animals. The author observed a tube-building species of Stentor which was very clearly marked with carbon in one experiment. Investigators of sponges have fed them carmine for various purposes, and it may be that some of their data can be used for determination of natural growth rates.

RESULTS OF EXPERIMENTS

Six marking experiments were made in the Bird Preserve Pond. Table 4 serves as a description of

TABLE 4. Data on the six attempted marking experiments in Bird Preserve Pond.

Experiment	Date marked	Date collected	Time started (E.S.T.)	Mean temperature °C.
1........	July 15, 1940	July 16	9:30 A.M.	18.2
2........	August 12, 1940	August 13	9:45 A.M.	24.6
3........	July 5, 1941	July 6	1:10 P.M.	22
4........	July 21, 1941	July 22	2:45 P.M.	..
5........	August 20, 1941	August 21	12:45 P.M.	24
6........	August 26*, 27, 28, 1941	August 29	12:45 P.M.	23

*The first mark in Experiment 6 cannot be seen on the tubes.

the experiments, giving the dates, duration, number of markings, and mean temperatures. For some unknown reason, Experiments 3 and 5 failed; carmine could not be found in the tubes. Nevertheless, the original numbering of the experiments is preserved, and further discussion will refer to the numbers given in Table 4. Experiment 6 was marked with carmine on August 26, 1941, with carbon on August 27, and with a mixture of the two on August 28; the experiment was terminated on August 29. Here, too, carmine could not be seen, but there were two very prominent black bands on the long tubes. Therefore, information is available for two successive days in Experiment 6. *Ptygura longicornis bispicata* and *Beauchampia crucigera* were marked with carbon in this experiment also. To summarize, information was obtained about *Floscularia conifera* from Experiments 1, 2, 4 and 6, and about *Beauchampia crucigera* and *Ptygura longicornis bispicata* from Experiment 6. In Experiments 4 and 6, the plant was divided into sections of five and ten leaves, respectively, and the rotifers from each section were kept separate.

In the discussion, a simple, rather arbitrary terminology will be used to describe animals of different ages. A larva is one of the free swimming animals before attachment to the substrate. A young animal is an attached one which is less than twenty-four hours old, while an adult is more than twenty-four hours old, or with at least one mark on the tube. This does not necessarily refer to the state of maturity. The term mature animal will refer to those old enough to lay eggs when this is specifically meant.

Floscularia conifera

Experiment 1

The results of this twenty-four hour experiment were briefly reported at the meeting of the Limnological Society of America in Philadelphia, Pennsylvania on December 28, 1940. Growth rate, ex-
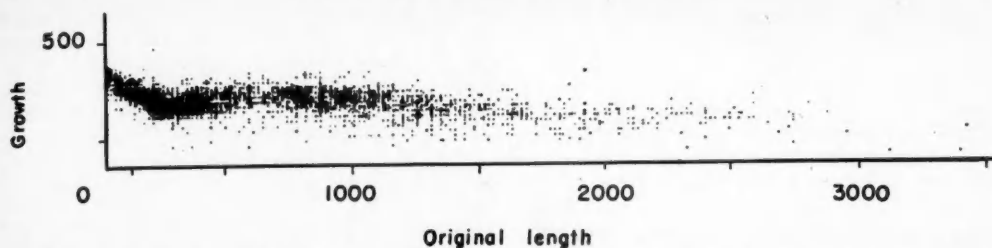
FIG. 9. Relation between length of tubes at the beginning of Experiment 1 and the amount of growth during the subsequent twenty-four hours. Each point represents an individual. Measurements in micra.

pressed in terms of micra per day, is simply the increment in tube length. The mean growth rate of all animals alive at the beginning of the experiment was 248 micra per day. In order to see whether growth rate varied with initial size, Figures 9 and 10 were made. These show that young animals tend
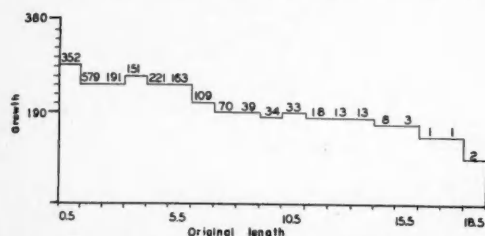
FIG. 10. The data of Fig. 9 grouped by size classes in a frequency histogram. The figures on the ordinate are micra, while those on the abscissa designate midpoints of size groups in terms of micrometer measurements where $1.0 = 191\mu$. The number of animals in each size class is shown over the line.

to grow a little faster than older individuals, but that the growth rate is relatively uniform during a large portion of the life span. There is considerable spread of points in Figure 9, indicating individual variability in growth rate. Doubtless many of the lowest points represent sick or dying animals. The mean size of animals alive at the end of the experiment was 642μ, equivalent to a mean age of 2.6 days. The largest animal alive at the end of the experiment was $3,550\mu$ long, or about 14.3 days old. *Floscularia conifera* rarely grows larger than 3 mm., and this is the largest individual ever seen by the author.

There were 2,672 animals alive on the entire plant at the beginning of the experiment. During the subsequent twenty-four hours, 1,292 young individuals became attached. This is an equivalent to an apparent reproductive rate of 48% per day; that is, the number of animals produced during twenty-four hours was 48% of the number originally present. Since many members of the initial population were very young and had not yet started to reproduce, an attempt was made to estimate the size of the initial mature population. The smallest rotifer seen to have an egg in this experiment was taken to represent the size at maturity. It was 420μ long, equivalent to an age of about 1.7 days. Counting all animals this

size or larger, there were 1,508 mature animals when the experiment started. This gives the apparent reproductive rate of the mature population as 86% per day. It may be useful to calculate the rate on still another basis, and that is for the mean number of mature animals alive during the experiment, since undoubtedly some reproducing individuals died. There were 2,238 mature animals at the end, which made the mean number 1,873, and the corresponding rate was 70% per day. The differences in these three rates reflect the age composition of the population and are useful for comparison with other populations.

The death rate was calculated by dividing the number of animals alive at the beginning of the experiment into the number that died during the twenty-four hour period. Since only 46 of the original animals died, the rate was 2% per day. Of the 1,010 animals attaching during the experiment, 4, or 0.3% died.

Since the reproductive rate was much greater than the death rate, the population would be expected to increase at a rate of about 46% per day (Volterra & d'Ancona 1935). That this did not actually happen is shown by Figure 2, for immediately after Experiment 1, there was a drastic decline in the size of the population. The explanation is to be found in the results of the next experiment.

Experiment 2

The sample obtained in the second experiment, of twenty-four hours duration, contained few live animals, and little quantitative information can be obtained from it. Most of the many tubes collected were empty, and contained only the hard jaws of the rotifer left after decay of soft parts. Frequently there were diatoms and desmids in the tubes as well. Many of the animals evidently had died just before marking. Some which were still alive at the end of the period still had no carmine in the pellets. The mean twenty-four hour growth for twenty animals was 153μ. No reproductive nor death rates could be calculated, but reproduction was certainly low.

The chief interest in this material is that it gives an explanation for the sudden decline in population size after the middle of July, for some of the empty tubes contained objects which look very much like some of the sporozoan parasites familiar in other rotifers (Budde 1914). The objects have actually been seen inside of Floscularia, and there is little

doubt that they are protozoan parasites, although it is impossible from this material to identify them with any genera so far described. At least one dead animal in Experiment 1 contained a parasite. Material collected on July 25 appears to have no parasites, so that the epidemic must have developed very rapidly. It may have been limited to a part of the pond only.

Experiment 4

A plant was divided into sections of five leaves each, so that the distribution of animals along the axis of the plant could be determined. In all discussion and figures, each section is referred to by a Roman numeral followed by letter a or b, taken in order from the distal end of the plant. The sections are thus numbered Ia, Ib, IIa, IIb, etc. A Roman numeral standing alone refers to a group of ten leaves. This is done so that this experiment can easily be compared with Experiment 6 where sections of ten leaves were taken. Table 5 and Figure 11 give the data. For convenience, the different kinds of animals distinguishable are referred to by letters as follows:

D. Alive at beginning and end of experiment.

E. Alive at beginning, died before end.

G. Born during experiment, lived until end.

H. Born during experiment, died before end.

The types are lettered this way to bring the nomenclature into exact correspondence with that of the more extensive Experiment 6, which covered two days (Fig. 13). Thus, in both, a G animal was born less than twenty-four hours before the end of the experiment, while an E animal was alive at the beginning of the twenty-four hour period just prior to the end of the experiment. No doubt some of the D animals of this experiment correspond to A animals in Experiment 6, being more than twenty-four hours old, but it is not possible to distinguish them here.

TABLE 5. Distribution of *Floscularia conifera* on Utricularia in Experiment 4. The types of animals are defined in the text. Sections of the plant are groups of five leaves as in Table 2. The figures give the number of each type of animal in each section of the plant.

Type of animal	D	E	G	H	Total
Section of plant					
Ia	0	0	3	0	3
Ib	10	2	13	1	26
IIa	20	2	13	1	36
IIb	40	6	17	0	63
IIIa	70	7	2	0	79
IIIb	54	4	0	0	58
IVa	43	7	2	0	52
IVb	69	8	4	0	81
Va	45	7	9	0	61
Vb	43	1	5	0	49
VIa	31	3	8	0	42
VIb	18	5	6	0	29
VIIa	25	7	10	0	42
VIIb	23	3	4	0	30
Total	491	62	96	2	651

The mean growth rate for the entire population was 195μ per day. When the rate for each section of the plant is examined, it is seen that a marked depression in growth occurred near the middle of the plant. Minimum growth of 82μ per day occurred in section IIIb, while the fastest rate was in sections Ib and VIIa, 298μ and 325μ respectively. The difference between the last two numbers is not significant. Obviously there was something peculiar about the middle of the plant which prevented animals from growing at the normal rate. Figure 11 shows further that the number of D and E animals (initial population) was at a minimum in the sections of minimum growth.
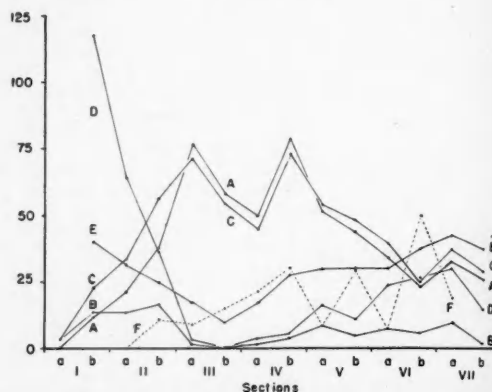
FIG. 11. Distribution of *Floscularia conifera* along the axis of the plant in Experiment 4 which was divided into groups of five leaves, designated by a Roman numeral and a letter. A, number of animals alive at beginning of experiment; B, number of young animals attaching during experiment; C, number of animals alive at end of experiment; D, apparent reproductive rate as per cent per day; E, growth rate as micra per day, $\times$ 0.12; F, mean number of eggs per original animal at end of experiment, $\times$ 100.

The apparent reproductive rate, calculated for the whole population, was 17.7% per day, but when it was calculated for each section separately, a strong depression was found in the section where growth was at a minimum. This apparent rate of reproduction was obtained by dividing the sum of D and E animals (alive at beginning) in a section into the sum of G and H animals (born during experiment) in the same section. As Figure 11 shows, the apparent reproductive rate was very high near the distal end of the plant, was reduced to zero in section IIIb for which it rose irregularly. Now it is unlikely that the animals in the middle of the plant actually were not reproducing at all, especially since there was a large supply of unhatched eggs in those sections as shown by line F in Figure 11. The number of larvae expected to settle in any section can be calculated if it is assumed that the actual reproductive rate to be constant in all parts of the plant, and further that there was no migration from one part of the plant to another, by multiplying the general
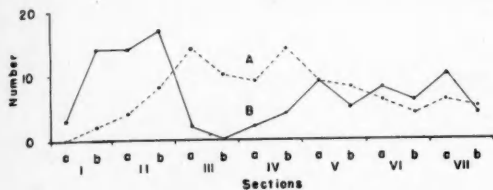
FIG. 12. Distribution of young *Floscularia conifera* attaching during Experiment 4 along the plant which was divided into groups of five leaves. A, number calculated in each section on the basis of mean apparent reproductive rate and the distribution of the initial population; B, number actually observed in each section.

reproductive rate (17.7% per day) by the number of animals initially present in each section. The number of young actually attaching is known from observation. If these be compared as in Figure 12, one gets the impression that larvae have fled from the middle sections, and crowded forward into four distal sections and, to some extent, into the proximal sections. There was a marked depression in death rate in Section V, but otherwise it varied irregularly and showed no correlation with growth or reproductive rates.

Clearly there was something abnormal about the conditions that surrounded the population, evidently some highly localized condition which was very unfavorable to both larvae and adults. The nature of this condition is a complete mystery to the author, and no explanation is offered. The existence of a minimum in numbers of A and B animals in the middle of the plant shows that depressive conditions had existed for some time before the experiment. Since this minimum was in the section behind the one in which the minimum of growth and settling took place, and since, as will be seen, Utricularia was growing at the rate of about 3.2 leaves per day, it seems that the depressive action had been going on for a day or two before the experiment began, perhaps three as a maximum. This rules out any chemical conditions in the water, since a localization of concentration would probably be dispersed in a short time.

Just how accurate the calculated reproductive rate for the population as a whole is can only be guessed. If the disturbing condition did not kill larvae, but simply repelled them from one part of the plant to another, the rate is correct. But if there was abnormal mortality or lateral migration of larvae, the rate is too low.

A fair number of tubes contained a ploimate rotifer which appeared to be *Proales decipiens*. These evidently had eaten the dead Floscularia. *Proales decipiens* is well known as a scavenger, as it is frequently found inside dead aquatic insect larvae, where it scrapes up the decaying tissues. However, in Experiment 6, a Proales was found in the act of attacking with the trophi an apparently healthy Floscularia. Nevertheless, there is no reason to think

that Proales is responsible for much mortality in Floscularia.

Experiment 6

This experiment, which lasted effectively for forty-eight hours, was the best performed so far, and gave most information about what may be presumed to be the usual distribution along the plant and about colony formation. Although the population was marked three times, only the last two marks were visible. The plant was divided into sections of ten leaves each which are referred to by Roman numerals starting at the distal end. There were 56 leaves, thus five complete sections and one composed of 6 leaves. Eight types of animals are distinguishable.

A. Alive at beginning and end of experiment.

B. Alive at beginning, died during first day.

C. Alive at beginning, died during second day.

D. Born during first day, lived until end of experiment.

E. Born during first day, died same day.

F. Born during first day, died second day.

G. Born during second day, lived until end.

H. Born during second day, died same day.

The appearance of each type of animal is shown diagrammatically in Figure 13, and the distribution on the plant in Table 6.

TABLE 6. Distribution of *Floscularia conifera* on Utricularia in Experiment 6. The types of animals are defined in the test. Sections of the plant are groups of ten leaves in order from the growing tip of the plant.

Type of animal	A	B	C	D	E	F	G	H	Total
Section of plant									
I	0	0	0	1	1	0	0	0	2
II	14	2	0	25	0	0	19	0	60
III	91	10	9	145	0	1	136	0	392
IV	152	22	6	213	0	5	202	2	602
V	73	12	10	119	0	2	94	0	310
VI*	24	0	3	24	0	0	21	0	72
Total.......	354	46	28	527	1	8	472	2	1438

*Section VI had only six leaves.

The mean growth rate was the same on both days, 334µ per day. This applies of course to A animals only. There was no significant difference in growth date in different sections of the plant, although there were small variations. The mean size of animals alive at the end of the experiment was 598µ, and this corresponded to a mean age of 1.8 days. The largest animal was 2,100µ long, which corresponded to an age of about 6.3 days.

The reproductive rate over the entire experimental period, calculated by dividing the sum of A, B and C animals into the sum of D, E, F, G and H animals and dividing by 2, was 117.7% per day. Calculated separately for the two days, using appropriate fractions, the rates were 125.2% per day for the first and 108.4% per day for the second day. While this is a fairly large difference, it probably means merely
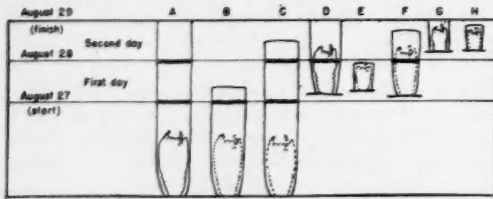
FIG. 13. Diagrammatic representation of the appearance of the categories of *Floscularia conifera* in Experiments 1 and 6, as defined in the text. Animals dead at the end of the experiment are shown in dotted line, those that were alive in solid line.

that immature animals were being added at a faster rate than young animals were maturing. The reproductive rate may also be calculated on the basis of number of mature animals present at the beginning of the period considered. The smallest animal to have an egg was 611µ long rather than 420µ as in Experiment 1, and was therefore about 1.8 days old. If this is taken as the length at maturity, there were 181 mature animals at the beginning of the experiment, 444 at the end of the first day, and 492 at the end of the experiment. Several reproductive rates can be based on these figures.

Rates based on number of mature animals at beginning of period: first day, 296.1% per day; second day, 106.7% per day; both days together, 276.2% per day. Rates based on mean number of mature animals alive at beginning and end of period: first day, 171.2% per day; second day 101.3% per day; both days together, 150.7% per day. Rate based on mean number of mature animals alive at beginning, middle and end of experiment, 135.7% per day.

Reproduction was at a considerably lower rate during the second day. The differences between the results of different methods of calculation arise in differences in number of mature animals at different times.

The death rate of animals alive at the beginning, calculated over the entire two-day period, was 8.6% per day. The death rate of the young animals settling during the experiment was 1.0%, since only 10 of the 1,010 young died. The death rate of animals, alive at the beginning, during the first day was 10.7% per day, and during the second day was 6.5% per day. The date during the first day for animals born during that day was 0.2% per day; the rate during the second day for these was 1.4% per day. Some of this variation was doubtless due to the small numbers involved, but there seemed to be a definite increase in death rate between the first and second day of life. This is treated more completely in a subsequent section.

The distribution of animals along the plant may now be considered. Data are given in Table 6 and Figure 14. The total number of animals at the end of the experiment rose from only one living individual in section I of the plant to a maximum of 567 in section IV, then fell abruptly. The apparent reproductive rate fell gradually toward the proximal end
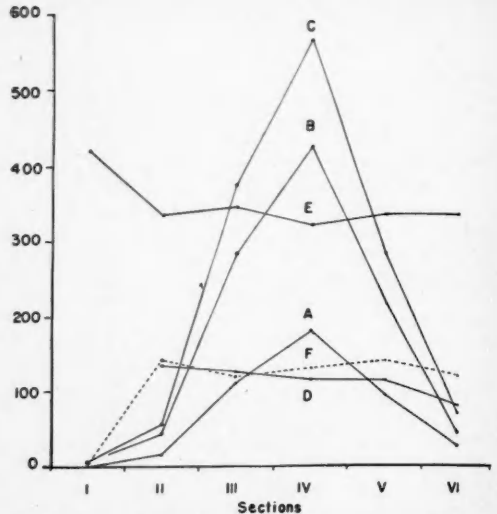
FIG. 14. Distribution of *Floscularia conifera* along the axis of the plant in Experiment 6 which was divided into sections of ten leaves each designated by Roman numerals. A, number of animals alive at beginning of experiment; B, number of young animals attaching during experiment; C, number of animals alive at end of experiment; D, apparent reproductive rate as per cent per day; E, growth rate as micra per day; F, mean number of unhatched eggs per original animal, at end of experiment, × 100.

of the plant. The number of eggs per individual was rather uniform, with a slight minimum in section III. The young animal in section I had no eggs. As in Experiment 4, it was unlikely therefore that the animals in the distal sections were reproducing faster than those in the proximal, especially as there are more young animals at the distal end. This suggests that there was a slight migration of animals toward the distal end of the plant. Now the number of young expected to settle in each section can be calculated on the basis of the number of animals initially present and the general reproductive rate of the whole population. Such calculated numbers can be compared with those observed. This is done in Figure 15. More young settled in the first four sections of the plant and fewer in the other sections, and this suggests again a distal migration of larvae. Since the data calculated differed in a systematic way, from those observed, further analysis was made.

Various assumptions may be made about how much migration there has been in each direction along the axis of the plant, and the resulting distributions tested against observed data. The reproductive rate of 117.7% per day was used to calculate the number of larvae produced in each section by multiplying it by the number of animals living in each section at the beginning of the experiment, and then multiplying this by 2 since the experiment, lasted two days. Further calculations were made by assuming that various percentages of the animals migrated. Mi-
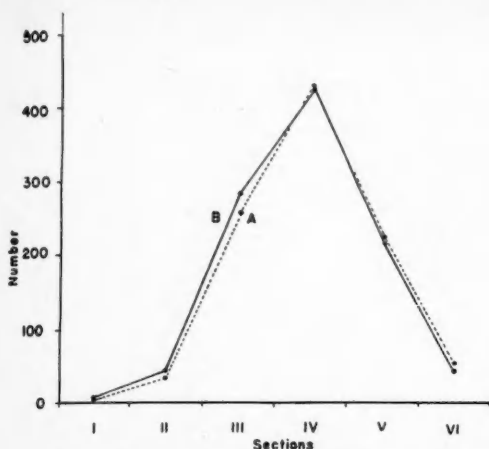
FIG. 15. Distribution of young *Floscularia conifera* as observed and calculated in Experiment 6. Explanation as in Fig. 12.

gration patterns were designated by three numbers which show, respectively, the percentage of larvae that moved distally into the adjacent section, the percentage that remained in the native section, and the percentage that moved back into the proximal adjacent section. Thus the symbol 10-85-5 means that 10% of the larvae born in one section went distally, 85% stayed where they were, and 5% went proximally. In order to decide which hypothetical migration pattern fitted the facts best, the observed number in each section of the plant was subtracted from the calculated number, and these differences added up for the whole plant regardless of sign. This was done for each migration pattern. In the list below are given first the designation of the migration pattern, next the sum of the differences between calculated and observed numbers of larvae for the plant, and finally the maximum difference in any one section.

Type of migration assumed	Sum of differences	Maximum difference
0–100– 0	61	23
5– 90– 5	79	27
10– 80–10	124	35
20– 60–20	210	71
30– 40–30	293	107
40– 20–40	379	143
50– 0–50	464	181
10– 85– 5	87	16
10– 90– 0	63	18
5– 95– 0	45	16
4– 96– 0	43	16
3– 97– 0	44	18

The closest fit to fact was obtained by assuming that about 4% of the larvae swam distally and the rest stayed where they were. Obviously this figure is approximate. In addition, other patterns than those shown were tried, but they gave large differences. Naturally this does not mean that the larvae never

swim toward the proximal end of the plant, but that any such migration is effectively overbalanced by distal movement. Moreover, migration means movement from one arbitrarily delimited section to another. A larva moving from leaf 20 to leaf 11 would not be recognized as having moved, although one that moved from leaf 11 to leaf 10 would. Nevertheless, as a whole, the tendency was for a certain fraction of the larvae to move distally in addition to any small to and fro motions along the plant.

The existence of distal migration can be seen to be of some importance to Floscularia, for if there were no such movement, new leaves would be unpopulated, and the plant would grow out from beneath the population. An explanation of the effectively unidirectional migration is therefore desirable. One thought that comes to mind is that larvae do not attach to heavily populated leaves, and so would tend to enter younger regions of the plant. This is not the case with Floscularia, for the animals do not simply move away from regions of densest population in both directions as would be expected if this were so; furthermore, there is no antagonism between adults and larvae, which frequently attach to adult tubes. While this sort of explanation does not apply to Floscularia, it should be kept in mind in the study of sessile populations, for it may well be that substrate competition does occur in some species. Data have been published which suggest that interspecific competition for substrate occurs in which Gloeotrichia is effective in crowding out Pelmatohydra, which will not attach to the alga (Miller 1936, Young 1941).

It is obvious, from microscopic examination of the behavior of Floscularia larvae in a Syracuse dish with a bit of Utricularia leaf, that they do not move at random. They swim toward the light when free of substrate, but when in contact with the plant, they move over its surface in a seemingly purposeful manner. Experiments show that *Floscularia conifera* larvae tend to attach in greater numbers to young leaves than to old ones (Edmondson 1944). It is evident to the eye that older Utricularia leaves bear more minute periphyton than do younger ones. Small bacterial organisms, for instance, are much more abundant on older leaves, as well as algae including Oedogoniales and such surface obscuring forms as Aphanocapsa and Gloeocapsa. It is probably a fair assumption that leaves which are covered with a fine fuzz of bacteria and are bristling with filamentous algae are not as suitable for sessility as cleaner ones. If the rotifer larvae are capable of differentiating between leaves of different texture and of making appropriate responses, the migration has a simple physiological basis. A larva which finds itself coming into contact with progressively more unsuitable substrate will probably turn and change its direction. Such behavior would be analogous to that shown by flatworms in a light gradient as discussed extensively by Frankel & Gunn (1940). Floscularia larvae have been observed to swim more than 5 cm. in a Syracuse dish, and it is certain that they are capable of swimming farther; thus they could come into contact with

several leaves before settling. Whether *Floscularia conifera* shows any reaction to the chemical nature of the leaves is unknown, but it seems unlikely that it reacts to the same stimuli which affect *Collotheca gracilipes* so strongly.

A possibility that must not be overlooked is that larvae swimming into unfavorable territory might leave the plant completely and swim to another. If true, one would expect immigration from other plants as well, and the larvae would approach all parts of the new plant, settling on the more suitable leaves. The fact that the entire first ten leaves of the plant in Experiment 6 had only 2 animals shows that considerable immigration is unlikely, although these two may have been immigrants.

Beauchampia crucigera

Most of the specimens found in Experiment 6 had two clearly defined black bands, indicating that they had existed since the time of the first carbon marking. Large specimens had the bands very close together or fused into one, and the specimens of largest size had only an ill-defined mass of black at the top of the tube. Evidently tube formation stops some time before the animal dies; the animal itself does not stop growing, since large animals extend much farther out of the tube than do small individuals.

The mean growth rate for the two days for specimens with two clearly defined bands was 111μ for the first day, 94μ for the second. This difference probably is not significant. Young individuals are very small, and it is possible that many were overlooked in dissecting the plant. The apparent reproductive rate calculated for the first day only on the basis of animals with one and two bands was 25.8% per day.

Table 7 and Figure 16 give data on the distribution along the plant. Here, as in *Floscularia conifera*, the maximum number was in section IV, but the distribution was different in that the slope of the curve is less steep in front of the maximum, steeper after it. If the migration of larvae is examined in the same way as was done with *Floscularia conifera*, the pattern 5-90-5 gives the best fit to facts, but actually the difference between this and 5-95-0 is quite insignificant, and no decision can be reached about the intensity of migration, since the population was too small to yield significant differences. Growth

and reproductive rates varied slightly and insignificantly from one end of the plant to the other.

Occasionally carmine stuck to the tube of this species in Experiment 4. The growth rate for nine specimens whose mean length at the end of the experiment was 400μ, was 88μ per day.
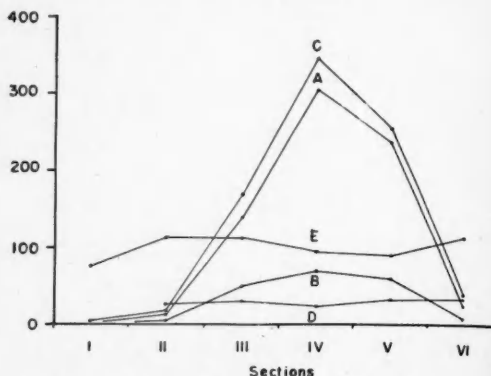
FIG. 16. Distribution of *Beauchampia crucigera* in Experiment 6. Explanation as in Fig. 14.

Ptygura longicornis bispicata

Ptygura longicornis bispicata occured in smaller numbers than either of the species discussed so far. As in Beauchampia, tube formation stops after a certain size or age is reached, while the animals continue to grow. The growth rate was 49μ for the first day of the experiment, 59μ for the second and was fairly regular along the plant. This difference is not significant, for the animals were measured only to the nearest 10μ.

The apparent reproductive rate for the first day was 24.6% per day for the entire plant. If the apparent rate for each section is calculated separately, a slight minimum is found (Table 8, Fig. 17). This

TABLE 7. Distribution of *Beauchampia crucigera* on Utricularia in Experiment 6. Explanation as in Table 6.

Type of animal	A	B	C	D	E	F	G	H	Total
Section of plant									
I	1	0	0	0	0	0	0	0	1
II	9	1	0	4	0	0	0	0	14
III	136	1	5	38	0	4	1	0	183
IV	284	6	14	64	0	6	11	0	385
V	197	12	27	55	0	6	3	0	300
VI	23	0	0	8	0	0	1	0	32
Total.......	650	20	46	167	0	16	16	0	915

TABLE 8. Distribution of *Ptygura longicornis bispicata* on Utricularia in Experiment 6. Explanation as in Table 6.

Type of animal	A	B	C	D	E	F	G	H	Total
Section of plant									
I	0	0	0	0	0	0	0	0	0
II	5	0	0	2	0	0	0	0	0
III	29	1	1	7	0	0	1	0	39
IV	100	1	0	16	0	0	6	0	123
V	45	1	0	17	0	2	2	0	67
VI	4	0	0	2	0	0	0	0	6
Total.......	183	3	1	44	0	2	9	0	242

irregularity is a result of the small size of the population. A satisfactory migration pattern can not be calculated for this reason, although an attempt was made with the result that more animals attached in section V, fewer in section IV than would be expected on any basis except preponderantly proximal
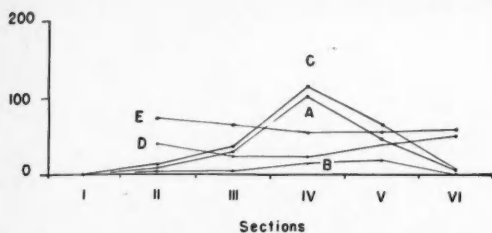
FIG. 17. Distribution of *Ptygura longicornis bispicata* in Experiment 6. Explanation as in Fig. 14.

migration, perhaps to the extent of 0-50-50 which fits fairly well. Whether this is a statistical artifact or an actual preference for attachment to algae and bacterial films cannot be determined from the data.

RELATIONSHIP BETWEEN THE RATES OF REPRODUCTION, SUBSTRATE GROWTH AND THE FORM OF POPULATIONS

The form of the distribution of sessile rotifers along a Utricularia plant would seem to be the result of several factors which operate to maintain a sort of steady state. The first factor is the reaction of larvae to leaves of different age, leading to a migration of varying intensity. The reaction may be elicited by the chemical nature of the leaves, as in *Collotheca gracilipes,* or by the amount of minute periphyton, as presumably in *Floscularia conifera.* The intensity of migration determines the characteristics, such as position of maximum and relative slopes, of the graph describing the distribution of the population. But these characteristics are modified by growth of the substrate. With constant rates of migration and reproduction of the fauna, the faster the plant grows, the farther back will be the maximum concentration of animals, and the gentler the slope of the graph. The height of the graph will depend on the reproductive rate. How much, if at all, the migration rate is influenced by the reproductive rate is not known. The three species studied in Experiment 6 may be examined. Since all the animals were on one plant, the effect of substrate growth was the same on all, and any differences in distribution must be a result of characteristics of the rotifers themselves.

To examine most simply the distribution of population in Experiment 6, shown in Figures 14, 16 and 17, the percentage of animals distal to the middle of the plant was calculated. Since section VI had only six leaves, the number of animals was multiplied by 10/6. Listed are first this percentage, then the reproductive rate as per cent per day, and finally the migration pattern as calculated previously.

Floscularia conifera 31   117.9   4-96- 0
Beauchampia crucigera 21   25.8   5-90- 5
Ptygura longicornis bispicata 18   24.6   0-50-50 (?)

Thus, in this experiment, there is a relation between the percentage of the population in the distal half of the plant and both the reproductive rate and migration patterns. In effect, none of the Floscularia

larvae swims far proximal on the plant, while some Beauchampia and many Ptygura larvae do.

The rate of Utricularia growth was determined on several occasions in a simple manner. A string or thread was tied loosely around the stem between the bud and first leaf. This was done without lifting the plant from the water or disturbing it more than necessary. Several days later the plant was recovered and the number of leaves between the string and bud counted. These leaves obviously were formed after the string was placed on the stem. Table 9 shows the results expressed in terms of leaves formed per day.

TABLE 9. Data on the growth rate of *Utricularia vulgaris americana.* The last column shows the section of plants collected at about the same time which contained the maximum number of *Floscularia conifera.* The sections are designated by a Roman numeral and letter as in Table 2.

Dates of beginning and end of experiment	Duration in days	Number of leaves formed	Rate, leaves per day	Mean Temperature	Population maximum
1940					
July 25-27..........	2.2	7	3.22	24.5	IIIa
July 27-August 7....	11.2	34	3.09	23.7	IIIb-IVa
1941					
June 23-July 24.....	11.0	21	1.91	23.0	IIIb
July 4-August 21....	48.0	85*	1.77	ca. 23	(IIb)
		156**	3.25		
August 28-Sept. 6...	9.0	25*	2.77	23	(IIIa)
		35**	3.88		

*Determination for main bud only.
**Determination for entire plant including side buds.

It is interesting to compare the location of the maximum rotifer population on plants collected during or near the times when these rates were determined. Unfortunately the lack of complete coincidence of measurements of Utricularia growth and population form prevent very exact evaluation of the relationship, but there is a tendency for the maximum to be further back on the plant when the growth rate is highest. In this comparison the rate of growth of the main stem is relevant.

In a specific study of the relationship between ages of different sections of the substrate and of the Floscularia population in each section, the mean, minimum and maximum ages of the rotifers alive at the end of the experiment and of the plant in Experiment 6 were calculated. These are listed, with ages given in days:

SECTION	FLOSCULARIA			UTRICULARIA		
	min.	mean	max.	min.	mean	max.
I	2.2	2.2	2.2	0.0	1.6	3.1
II	0.5	1.7	5.0	3.1	4.7	6.3
III	0.2	1.8	6.1	6.3	7.8	9.4
IV	0.2	1.7	6.3	9.4	10.9	12.5
V	0.3	1.9	6.1	12.5	14.0	15.6
VI	0.3	1.8	5.5	15.6	16.4	17.2

Fig. 18 shows the data graphically. The mean rotifer age is smallest in section II, but rises only slightly and insignificantly toward the proximal end of the plant. The maximum rotifer age is greatest in section IV, and falls somewhat proximally; it is larger

than the minimum plant age in the first two sections only. The age of the animal in section I suggests that it was an immigrant from another plant, or swam exceptionally far distally on this plant. Thus *Floscularia conifera* does not have such a sharply differentiated age distribution along the plant as does *Collotheca gracilipes.* This fact probably results from the much smaller intensity of migration toward the distal end of the plant.
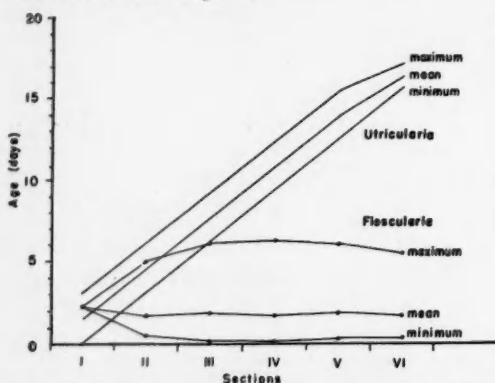
FIG. 13. Maximum, mean and minimum ages of *Floscularia conifera* and *Utricularia vulgaris americana* for each section of Utricularia in Experiment 6. The maximum and minimum ages of a Utricularia section are the ages of the oldest and youngest leaves, respectively.

These results are of more general interest in connection with some work by Burkenroad on the sessile fauna of various forms of Sargassum in the North Atlantic Ocean. "Almost every individual plant of eupelagic Sargassum is overgrown by some one of a limited number of species of colonial epizoan which, upon the outer and younger portions of the plant at least, dominates the attached fauna" (Parr 1939: 23-25). Sargassum is similar to Utricularia in that it grows actively in one or more terminal portions, the older parts breaking off and sinking. "Experiments made at the Bermuda Biological Station in 1936 suggest that the specificity of the exclusiveness of the dominant is not an immediate effect of the substratum . . . or of the epizoan association. . . ."

Burkenroad's hypothesis is that the various hydroid species, which reproduce exclusively by asexual budding on pelagic Sargassum, have different rates of growth, and that the various forms of Sargassum also grow at different rates. Thus if a slow-growing hydroid should become planted on a fast-growing plant, it would not be able to maintain itself on the younger parts of the plant, and would be left behind on the older parts where it would eventually be lost by sinking. Such an animal might be able to maintain itself on a more slowly growing substrate. On the other hand, a fast-growing animal could keep up with a fast-growing substrate. To explain why slow-growing plants are not overgrown by fast-growing animals, Burkenroad assumes that slow-growing hy-

droids are more efficient feeders in the presence of which fast-growing types cannot maintain themselves. This paradoxical assumption is resolved by considering the shapes of the presumed fast- and slow-growing hydroids. The species which are supposed to be fast growing are invariably long, slender colonies with sparsely distributed hydranths, while those that are supposed to grow slowly are more massive colonies with the hydranths closer together, forming a more efficient looking filter. It should be noted that growth, as used in this connection, refers to the rate of linear extent, not volumetric increase. Therefore, even if the volumetric increase were the same in both types of hydroids, the slender forms would cover a greater area of plant. Unfortunately, there are as yet no critical experiments on the competitive relationships between these forms, and this is the weakest part of the hypothesis. Evidently nothing is known about the possibility of a preference for the fresher parts of the plant, and substrate preference has not been clearly ruled out by the experiments.

The form of the distribution of sessile rotifers on Utricularia in Experiment 6 indicates that Burkenroad's explanation of the distribution of hydroids on Sargassum may be sound as far as it concerns the relative rates of growth. The reproductive rate of the rotifers appears to be analogous to the volumetric growth rate of hydroids, while migration of rotifers is comparable to linear extension of hydroids. Here the substrate growth under all species is the same, but as far as can be seen, the species with the fastest reproduction and most extensive forward migration has a greater portion of its population distal to the middle of the plant. We can imagine a case where, with the rate of migration found in Experiment 6, a plant might grow so fast that the rotifers would be left on the proximal part of the plant. If the plant were disintegrating proximally as rapidly as it was growing distally, the population might disappear from the plant. There are no direct measures of the rate and extent of migration in the present experiments. However, about 4% of the young in Experiment 6 swam far enough to enter the next ten-leaf section. Since the mean distance from one such section to the nearest leaf of the next is five leaves, we may assume that about 4% of the young swim a distance equivalent to five leaves or more before settling. Thus we might expect a Utricularia growing faster than five leaves per day to lose its Floscularia population unless migration were greater than in Experiment 6. The maximum rate yet measured was nearly four leaves per day. Since the linear distance between leaves probably varies with the growth rate, this is a pretty rough approximation, but it serves as an indication of the order of magnitude of the critical growth rate in this case.

RATE OF PRODUCTION AND DEVELOPMENT OF EGGS IN FLOSCULARIA CONIFERA

The marking experiments which have been described give information about the rate of settling of young, but no indication of the degree of embryonic and larval mortality. Therefore, it is desirable to

TABLE 10. Length and age frequency distribution of *Floscularia conifera* in Experiments 1 and 6, classified by the number of unhatched eggs contained in tube. The size range is given in micrometer units where $1.0 = 191\mu$. The equivalent age in days of the upper limit of each size interval is given.

| Size | Age | EXPERIMENT 1 Number of Eggs | | | | | | | | Age | EXPERIMENT 6 Number of Eggs | | | | |
		0	1	2	3	4	5	6	7		0	1	2	3	4
0.0 - 1.0	0.77	248	..	..	..	..	..	..	..	0.59	86	..	..	..	..
1.1 - 2.0	1.54	1172	1	..	..	..	..	..	..	1.18	370	..	..	..	..
2.1 - 3.0	2.31	875	4	1	1	..	..	..	..	1.76	312	2	..	..	..
3.1 - 4.0	3.08	284	3	1	1	..	..	..	..	2.35	216	19	3	..	..
4.1 - 5.0	3.84	142	22	5	1	..	..	..	..	2.94	61	44	20	3	..
5.1 - 6.0	4.61	121	158	31	6	1	..	1	..	3.52	6	8	26	16	..
6.1 - 7.0	5.38	31	151	104	13	0	..	..	1	4.12	3	2	18	19	3
7.1 - 8.0	6.15	11	80	93	12	1	1	..	1	4.70	6	9	14	17	6
8.1 - 9.0	6.92	11	34	77	9	1	..	..	..	5.29	1	2	8	15	3
9.1 - 10.0	7.69	5	27	55	3	3	..	..	..	5.89	..	2	1	5	1
10.1 - 11.0	8.45	3	17	35	2	1	..	..	..	6.47	..	..	1	3	..
11.1 - 12.0	9.23	5	7	34	3	..	..	..	..						
12.1 - 13.0	9.99	0	12	13	4	..	..	..	..						
13.1 - 14.0	10.77	1	8	5	..	..	..	..	..						
14.1 - 15.0	11.54	2	8	6	..	..	..	..	..						
15.1 - 16.0	12.30	1	3	3	..	..	..	..	..						
16.1 - 17.0	13.07	..	1	2	..	..	..	..	..						
17.1 - 18.0	13.84	..	..	0	..	..	..	..	..						
18.1 - 19.0	14.61	..	..	1	..	..	..	..	..						

seek further for information about fecundity; that is, the rate of egg production. The number of eggs in the tube of an animal is a function of the rates of production and development of the eggs and of the age of the animal. In the absence of direct measurements of the two rates, estimates can be based on the ages of tubes containing various numbers of eggs. The ages are estimated from size and mean growth rate. Table 10 shows length frequency distributions of Floscularia tubes classified according to the number of eggs they contained.

The discussion can most easily proceed by consideration first of the history of one animal under various conditions, and by reasoning from that to the populations as represented by Table 10. The discussion will be simplified, to the eye at least, if various cumbersome phrases are represented by symbols:

T, mean time between laying of successive eggs.
L, mean time required for eggs to develop.
A, age of animal from hatching.
a, age of animal from laying of first egg.
n, number of unhatched eggs in tube at any time.
N, maximum number of eggs observed in tubes.
ΔA, length of age or size class in distributions such as in Table 10, where it is 191μ, or 0.77 and 0.59 days in Experiments 1 and 6, respectively.

Now it is easily seen that if $T \geq L$, there can never be more than one egg in the tube at a time, and many animals in a population will have no egg for part of the time. The fraction of time that any individual animal has an egg is the same as the fraction of a population that has eggs at any time, and is L/T, providing that the laying and hatching are not confined to one part of the day. The fraction without eggs is $1 - L/T$. Both populations in Table 10 had many animals with more than one egg; there-

fore, $T < L$. In other words, in the experiments the mean length of time between the laying of eggs was less than the length of embryonic life, so that eggs could accumulate in the tubes up to a point.

As an animal ages after reaching maturity, the number of unhatched eggs should increase until a = L, at which time the number of eggs is at a maximum (N) and equals L/T. If L is not evenly divisible by T, n will fluctuate between the nearest two whole numbers. In fact, with natural variation in the rate of production and development of eggs, N will be expected to fluctuate anyway.

If, in a frequency table such as Table 10, the age (size) interval ΔA is very small compared to the absolute value of T or time interval between eggs, then the minimum size of animals containing progressively greater numbers of eggs should itself progressively increase as long as T and L are relatively constant. If $\Delta A/L \geq N$, the minimum size of animals containing eggs will be the same for all animals regardless of how many eggs they are carrying. If $\Delta A/L$ is slightly less than N, several egg classes will have the same minimum size. Table 10 shows that in both populations, L must be considerably larger than ΔA, since the minimum increases markedly with the number of eggs. In other words, the time required for the eggs to develop is considerably longer than 0.8 and 0.6 days in Experiments 1 and 6 respectively. There is a general and rather regular increase in the minimum size of animals from one egg class to the next. Some irregularity is seen in Experiment 1, where the only animal with five eggs was older than expected, but this kind of discrepancy is to be expected when the number of individuals is so small. The period of immaturity, during which no eggs were laid, was about 1.5 days in both experiments. This agrees fairly well with the previous

estimates based on the size of the smallest animal with an egg.

It should be noted that the appearance of Table 10 could be simulated, even if T and L were very short, if the ratio T/L varied. The ratio would have to be less than 1 during early life, so that there would be but one egg in the tube at any time. Then the ratio would increase as the animal aged, and n would consequently increase progressively. The change in value of the ratio implies increase in L or decrease in T or both. It is known that both of these values increase in *Proales sordida* and some other rotifers (Jennings & Lynch 1928). Therefore, a decrease in T (time between eggs) is unlikely here, although it might remain nearly constant. In any case, L (length of time of development) would have to increase by 800% in Experiment 1, by 500% in Experiment 6 between the time of laying the first egg and the time of achieving the greatest number of eggs possible (N), or even more if T were increasing. This is physiologically very unlikely. The largest increase observed in *Proales sordida* was about 11%. It therefore appears probable that T and L are large compared to ΔA, and that the numerical values can be estimated.

The mean rate of egg production can be roughly calculated by dividing N by the difference between the age of the youngest animal containing N eggs and the age of the youngest animal observed to have one egg. Using the mid-points of the size classes in Experiment 1 as measures of these ages, 7 eggs were produced in a time equivalent to 3.8 days. Thus, there was a mean interval of 0.55 days between eggs (T). If animals with more than 4 eggs are neglected in the calculation because of the irregularity in higher numbers, the time (T) is 0.77 days. This assumption is probably unjustified. In Experiment 1, the youngest animal to have N eggs was about 4.9 days old. For Experiment 6, T is 0.59 days per egg, and the smallest animal to have N eggs was 3.8 days old. The rate of egg laying, 1/T, is 1.81 and 1.69 eggs per day for Experiments 1 and 6, respectively. Thus the two populations agree very closely in length of period of immaturity and age at which N eggs appeared in the tube. The rate of egg laying was slightly higher in Experiment 1, but from the nature of the data, the difference may not be significant.

It is interesting to compare the rates of reproduction, which may be expressed as 181% and 169% per day respectively, with the apparent rates as determined by the marking experiments. The rate of settling calculated for Experiment 1 was only 48% per day. This is equivalent to a total embryonic and larval mortality of 73% per day ($\frac{181\text{-}48}{181}$). The rate of settling in Experiment 6 was 118% per day. Here the embryonic and larval mortality amount to 30% per day ($\frac{169\text{-}118}{169}$). Of course, some of the apparent mortality may be emigration from the plant that is not balanced by equal immigration. It appears then that the chief difference between the two populations is that some condition led to higher em-

bryonic or larval mortality or emigration in Experiment 1.

With these estimates of egg production, one can now estimate the length of the embryonic period, L. Since N = L/T, L = NT. For Experiment 1 this is 3.8 days using the most likely value of T, 3.1 using the other. For Experiment 6 it is 2.4 days. The times are quite different and rather higher than might be expected from what is known of other rotifers. Jennings & Lynch found that L in *Proales sordida* was 20.5 hours for eggs laid by young parents, 22.8 hours for eggs laid by old ones. Moreover, compared to Proales, Floscularia lays eggs very slowly. *P. sordida* laid about 9 eggs per day when young, 1 per day when quite old.

It is possible to arrive at a limiting value of the length of embryonic development (L) quite independently of that already given. In Experiment 6, there were 4 Type B animals, as already defined, with one egg and 3 with 2 eggs. Since these animals had been dead for more than 24 hours and less than 48, it must take at least a day for eggs to develop. Of all tubes seen which had been vacated before the experiment began, one contained an egg just ready to hatch, judging by the appearance of the embryo. All that is known of the age of this egg is that it was more than 48 hours old. This is probably a minimal estimate, for unfortunately no special effort was made to retain all the very old, empty tubes while dissecting the Utricularia. Therefore, no special stress need be placed on the fact that only one egg older than 48 hours was seen. If all old, empty tubes could have been examined, and this was still the only one with an egg, it would then seem likely that this was an especially slowly developing or dead egg, and L under those conditions would necessarily be less than 48 hours. In any case, this direct determination supports the order of magnitude for L previously deduced. The very long L in Experiment 1 is possibly a matter of temperature, since the water was 5° C. cooler than in Experiment 6.

The length of the period of fecundity may next be examined. If, after the maximum number of eggs N is attained, L and T remain rather constant for a considerable time, the number of eggs should remain at N, with possible fluctuations toward the next lower and higher numbers. If egg production is suddenly stopped, at a time about L later n will start declining at approximately the same rate at which it was attained in youth. But if L or T increase progressively, as is more likely, the rate of decrease will be slower. That is, if the animals lay eggs at a slower rate as they age, and if the eggs take longer to develop as in *Proales sordida*, the number of eggs in the tube will decrease at a slower rate than if egg production stopped suddenly. Extending these considerations to the population data, it is seen that n declined very soon after reaching N in Experiment 1, while it remained constant for 4 size classes or about two and a half days in Experiment 6 before declining very abruptly. To find the age at which reduced egg production started, L is subtracted from the age of the oldest animal to have

N eggs. This is about two days for Experiment 1, showing that the rate of production must have started falling from a high value very soon after maturity was reached. In Experiment 6, reduced egg production must have started when the animals were about three days old.

Apparently in Experiment 6 the animals continued to lay eggs, even though at a reduced rate, all through their lives, and there was no period of senility during which life continued but no eggs were laid. If there had been a long, well defined period with no egg production, the size distribution of animals with no eggs in the tube would be distinctly bimodal. This is not the case; if a period of senility exists, it must be shorter than the length of the embryonic period.

In reading the previous discussion, it should be remembered that all ages were estimated from the size of the animals and the mean growth rate. The individual variation in growth rate is so great that all derived ages and length of time are approximate. Nevertheless, it is believed that by using the midpoints of size classes rather than individual measurements wherever possible, some of this variation has been cancelled out and that the figures are representative.

The same four periods of life mentioned casually here have been established for a number of other rotifers including *Proales sordida* (Jennings & Lynch 1928). These are the periods of embryonic growth, immaturity, fecundity and senility or old age. The embryonic period is that between the laying and hatching of the egg from which the animal develops. The period of immaturity is ended with the laying of the animal's own first egg, and the period of fecundity is ended with the laying of the last egg. The period of senility is the rest of the life during which no eggs are laid. In *Proales sordida*, there is a very high death rate between the last two periods. In *Proales decipiens* this mortality is so high that no animals survive, and there is no period of senility. Jennings & Lynch suggest that the lack of senility in *P. decipiens* may be due to more rigorous culture conditions rather than to an inherent difference between the species. Neither population of *Floscularia conifera* described here can be said to have a proper period of senility, although the production of eggs was reduced much earlier in Experiment 6 than in Experiment 1.

It is instructive to compare in tabular form several characteristics of the life histories of a number of species (Table 11). Jennings & Lynch (1928: 372) summarize data published up to that time. Additional later references are given in Table 11 and in the bibliographies of these papers. In addition, data on *Lecane inermis* are given by Finesinger (1926) and on *Proales felis* by Bianco (1924). *Floscularia conifera* in natural populations is surpassed in length of life by only two of the other seven species in Table 11. However, bdelloid rotifers may tend to live longer than the Monogononta; Zelinka (1892) found two bdelloid species that lived five months in culture. The sessile *Cupelopagis vorax* lived 42 days

TABLE 11. Comparison of vital statistics of several species of Rotatoria. Data are for amictic females only, and concern laboratory cultures except in *Floscularia conifera*. Some values are means for several populations. All times are given in days.

	Floscularia conifera (Experiment 1)	Floscularia conifera (Experiment 6)	Proales sordida (Jennings and Lynch 1928)	Proales decipiens (Noyes 1922)	Lecane inermis (Miller 1930)	Epiphanes senta (Ferris 1932)	Epiphanes brachionus (Kolisko 1938)	Brachionus pala (Kolisko 1938)	Keratella aculeata (Kolisko 1938)
Maximum length of life from hatching	18.6	6.3	22	7	14	12	17	....	29
Mean length of life from hatching	2.6	1.8	7.4	5.5	ca. 7.4	8	8	5.8	22
Mean length of embryonic period	3.8	2.4	0.9	<1	1.5	0.9	....	....	....
Mean length of period of immaturity	1.7	1.8	0.9	1	ca. 1	1.7	3.8	2.6	3.9
Mean length of period of fecundity	....	....	ca. 5	ca. 5	6.4	3.4			
Mean length of period of senility	0	0	ca. 5	0	1.2	2.2	ca. 2	3	9
Mean number of eggs laid per day	1.5	1.4	ca. 3.5	ca. 4	3.2	....	0.8	1	
Maximum number of eggs produced during life	....	....	34	30	24	66	....	....	15
Mean number of eggs produced during life	....	....	24	20	20.7	45	4.3	3.6	8
Percent of eggs not hatching*	67	14	8	....	0.5	....	....	....	....

*Includes larval mortality in *Floscularia conifera*.

in culture (Cori 1925). There is considerable variation in other characters shown in the table, some of which may be caused by variations in culture technique. It is instructive in this regard to compare the work of Finesinger (1926) and Miller (1931) on *Lecane inermis*, although the papers were written from quite different points of view. The total number of eggs laid during the life varies from 5 in *Testudinella elliptica* (Lunz 1936) to 66 in *Epiphanes senta*. It should be noted that there is considerable variation in the literature in the manner of reporting the length of life. Sometimes the "mean length of life" appears to be actually the mean age of some of the longest lived individuals. Thus, the data in Table 11 may not be strictly comparable in all respects, but they illustrate pretty well the variation that exists. Some of the papers cited permit comparison of amictic females with mictic females or males.

SIZE DISTRIBUTION OF FLOSCULARIA CONIFERA

If *Floscularia conifera* hatched at regular intervals during the day and all individuals grew at precisely the same rate, the length frequency distribution of animals hatched during a given period of time would have, at the end of that time, the same number of individuals in each size class. A histogram of such data would be quite flat across the top. If hatching were regular, but growth rate varied slightly in a

random manner, the frequency distribution would still be almost flat across the top; the extreme size classes would contain fewer animals than the others, but the distribution would be symmetrical. Such size distributions were investigated in the experimental populations.

Consider first the length frequency distribution of young Floscularia, those which attached after the last marking and lived until the end of the experiment and therefore were less than twenty-four hours old (Fig. 19). In contrast to the foregoing theoretical distribution, these are neither flat nor symmetrical.
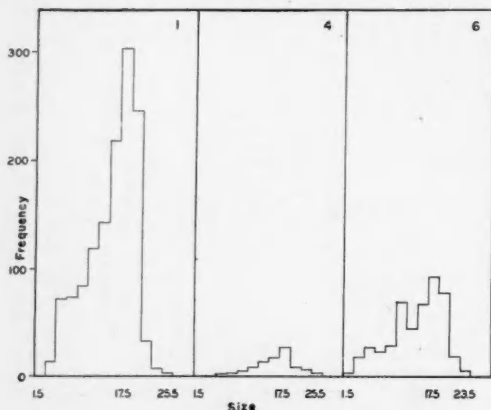
FIG. 19. Length-frequency distributions of young *Floscularia conifera* (less than twenty-four hours old) in Experiments 1, 4 and 6. Lengths are shown as midpoints of size classes in terms of micrometer measurements where $1.0 = 191\mu$, and each class is 38.2μ long.

There is a marked maximum in all experiments and each is highly skewed to the left, so that the mode is to the right of the middle of the size range. The animals should not be expected to grow at precisely the same rate, but the sharp maximum and asymmetry of the actual distributions require analysis.

If we assume temporarily that the size of an animal is an exact measure of its age, then the various size classes can be regarded as age classes, since the smallest animals settled just before collecting the population, and the largest just after marking twenty-four hours before. In that case, there must have been a maximum production of young at the time represented by the maximum frequency. These times were

Experiment 1 6:30 P.M. E.S.T.
Experiment 4 11:00 P.M. E.S.T.
Experiment 6 8:45 P.M. E.S.T.

Experiment 6 had a subsidiary maximum of doubtful significance at about 2:45 P.M.

Another possible explanation for the shape of the distribution may lie in the manner of growth. If, during the first twenty-four hours of life, the rate of growth abruptly increased from a very low value, an asymmetric distribution would be expected in a dia-

gram of the type of Figure 19, providing there was enough individual variation to account for the slope at the ends of the distribution. A morphological basis for such a change in growth rate is provided by the fact that the corona is undeveloped when the larva attaches, but after a few hours grows rapidly and is almost completely differentiated at the end of a day.

Now if the asymmetry were caused by variable production of larvae, a length frequency distribution of an entire population should show a series of decreasing maxima of frequency with increasing size. Moreover, if there is a maximal production every day, as suggested by the fact that all three experiments seem to have a maximum in the first part of the night, there should be one maximum for each day of age in the population. On the other hand, if the asymmetry and maximum are caused by anatomical or physiological factors, there should be no effect on the adult population histogram. Figure 20 shows
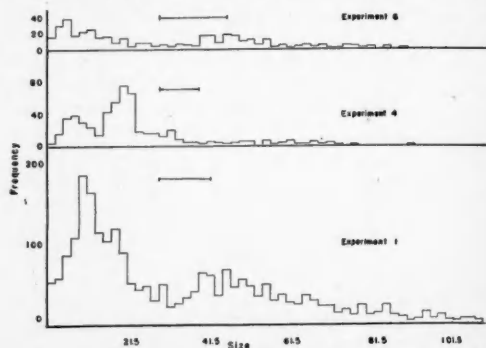
FIG. 20. Length-frequency distributions of the initial lengths of *Floscularia conifera* alive at the beginning of each experiment. The line above each histogram gives the size equivalent of one day of growth at the mean rate. Only part of the distribution of Experiment 1 is shown since there were a few very large animals. Other explanation as in Fig. 19.

such length frequency diagrams for the initial lengths in all three experiments; that is, of the population as it was at the time of first marking. The scale on each diagram shows the length corresponding to one day of growth at the mean rate. Each histogram has at least two maxima, but it is evident that they do not correspond to daily phenomena. For instance, it appears that the youngest maximum in Experiment 1 consisted of animals less than twenty-four hours old, while the older one consists of animals produced about two days before that. Notice that the youngest maximum in Experiment 4 is smaller than the next older one; this shows that there must have been heavy mortality or emigration or both during the last day before the experiment.

Experiment 6 has been analyzed further. Figure 21 shows the length frequency histogram for all animals alive at the end of the experiment, and this is broken down to show the contribution of A, D, and G animals to it, as defined in the first discussion of the experiment. There is some overlap between D and
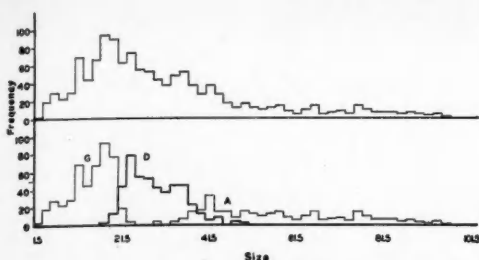
FIG. 21. Length-frequency distribution of *Floscularia conifera* alive at the end of Experiment 6. Above, total distribution. Below, the contribution of A, D, and G animals, as defined in text, to the distribution above. G and D animals are those hatched during the last two days of the experiment.

G, quite a bit between D and A. This overlap is a good measure of the departure of the growth rate from constancy at different ages. Note that the overlap animals are rather symmetrically distributed around the maximum.

It is noteworthy that the form of the maxima in Figure 20 is asymmetrical, but in the opposite direction from that in histograms of animals less than twenty-four hours old. A possible explanation is that the tube first formed by the newly attached animal is soft and somewhat compressible. That this is true is shown by the fact that basal pellets in old tubes are somewhat flattened. It is evident that only the part of the tube first formed is compressed, so compression does not occur through much of the life of the animal. The form of the histogram for the initial length of D and E animals (not figured) is flatter across the top and more nearly symmetrical than that for G animals in the same experiment, and suggests that compression stops before forty-eight hours. It is not clear, however, how such compression actually would result in a reversal of the direction of skew. It should be pointed out that the compression is so limited that growth rate determinations are not affected.

It seems likely then that the fundamental cause of the appearance of Fig. 19 and the maxima in Fig. 20 is either irregular settling of young or variations in the reproductive rate. The number of larvae settling could be affected by predation or by variable production of eggs following short time fluctuations in the abundance of food organisms. The fact that egg production in Experiment 1 was almost equal to that in Experiment 6, although the rates of settling were much different, suggests that the former explanation is most usual. The possible change in growth rate during the first day of life may contribute some effect. Perhaps the most direct way to attack this problem is to mark a population several times in one day.

COLONY FORMATION IN *FLOSCULARIA CONIFERA*: ECOLOGICAL ANALYSIS OF A LABILE SOCIAL STRUCTURE

Floscularia conifera often occurs in aggregations of different numbers. Young animals attach to the tubes of older individuals, and groups are built up (Fig. 7). These weak social structures of variable intensity invite analysis with reference to the effect of colonial habit on the life of the rotifers involved.

INTENSITY OF COLONY FORMATION

The first question that arises concerns the intensity of colony formation, or strength of the tendency to form colonies. One might expect a certain number of colonies to be formed by accident, simply by random distribution of larvae to all available substrates. If the distribution were random, concentration of animals on the surface of tubes should be about the same as on the surface of plants. Data to test this are drawn from a collection at Bird Preserve Pond on July 13, 1940 and from Experiment 1, on July 15-16, 1940. In the collection, 1,775 animals were directly attached to the plant, 651 to the tubes of some of these animals. The mean area of adult *Floscularia* tubes can be calculated from measurements of the experimental material. Assuming the mean size of adults to be about the same in both groups, as seems likely since they were collected only two days apart, we find that there were 1.55 cm.^{2} of tube surface attached to a plant whose area was 196 cm.^{2} The concentration of individuals on the two substrates was

> Attached to tubes   420 individuals per cm.^{2}
>
> Attached to plants   9 individuals per cm.^{2}

The rotifers were then more than 46 times as abundant on tubes as on the plant. Even if errors as great as 100% were made in measuring the surface of both tubes and plant, the concentration would still be at least ten times as great on the tubes. Evidently larvae actively attach to tubes in preference to Utricularia.

Wulfert (1939) claims that the larvae of *Floscularia ringens* always return to the mother animal and attach to her tube, although he gives no observational data to support this. Certainly it cannot be absolutely true for any species, for there would never be any solitary animals except those that hatched from resting eggs, and no forward migration. It may be true, however, that a large proportion of larvae attach immediately to the tube in which they were born, while most of the rest swim forward. The concentration of *Floscularia conifera* in colonies may be another example of substrate preference. Although it is possible that larvae are attracted to adults by ciliary currents, they swim strongly enough so that they cannot be swept helplessly into colonies.

The intensity of colony formation can be expressed in another way, by calculating the apparent reproductive rates for colonial and solitary animals separately. The young in a colony may be offspring of either solitary or colonial animals, and the difference between the two rates is a measure of the tendency to form colonies. The colonial rate, for instance, is calculated by dividing the number of initially colonial animals into the number entering colonies in a day. Below are listed the rates as per cent per day in the three experiments.

Experiment	Solitary	Colonial	Difference
1	44.6	49.4	4.8
4	16.8	24.5	7.7
6	80.8	126.2	45.4

It should be noted that there is considerable variation among the experiments with reference to the mean size of colonies also. The mean numbers of animals in the colony calculated for each experiment including solitary animals were 2.5, 1.1 and 3.4 in order. Neglecting the rather abnormal Experiment 4 from consideration since the population was obviously undergoing change and was subject to some undetermined depressive influence, the list given above suggests that colony size and the difference between apparent reproductive rates of solitary and colonial animals are related, as indeed they should be, but there is not a simple ratio.

Table 12 shows the two rates calculated separately for each section of the plant in Experiment 6. The rate is higher for colonies in all sections except the fifth. With this exception, the difference in rates increases toward the proximal end of the plant, suggesting that conditions were progressively unfavorable for attachment to old leaves. Evidently the tube offers a more constant substrate than the plant. This supports previous speculations about the cause and nature of distal migration and also the idea that colony formation is largely a matter of substrate preference. There are fewer animals in the distal section to which to attach, but that should not affect the percentage expressions unless the relation between attachment and area is not linear and a certain minimum amount of tube must be present before affecting the larvae.

The growth of colonies in number of animals dur-

TABLE 12. Apparent reproductive rate of solitary and colonial *Floscularia conifera* calculated separately for each section of the plant in Experiment 6.

Section of plant	Reproductive Rate (% per day) Solitary	Colonial	Difference
I	...	...	...
II	133	140	7
III	82	140	58
IV	66	126	60
V	135	109	− 24
VI	20	126	106

ing the experimental period was studied as a further expression of intensity of colony formation. Table 13 is a frequency distribution showing the increase during Experiment 6. There were 820 individuals which remained solitary during the period, while 170 added one or more young. While the intensity of colony formation in this experiment was obviously much higher than in the others, it may be regarded as typical of many populations, at least when the species is abundant.

GROWTH RATE

The effect of aggregation on growth rate can be most simply measured by calculating the mean growth rate for solitary animals and for colonial animals separately. In Experiment 1, the rates for adults were 248μ per day for single and 267μ per day for colonial animals. This difference is statistically insignificant by the t test. The rates for both single and colonial adults in Experiment 6 were 334μ per day.

TABLE 13. Frequency diagram showing the number of colonies of *Floscularia conifera* in Experiment 1 which increased from various initial sizes to the final sizes shown. Note that the scale for final size is broken above 20.

Original size of colony	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	24	25	26	30	34	36
1	820	136	29	4	1																					
2		37	47	44	9																					
3			17	32	33	7																				
4				13	10	12	5	1																		
5					8	8	14	5	1	2	1															
6						7	4	7	9	1																
7							6	3	6	5	1	2	2													
8								1	2	1	1	2														
9											3	2	1													
10												1	1	1												
11											1	1		1	1											
12														1	1											
13													1				1	1		1						
14														1					2	1						
15																		1								
16																1										
17																										
18																						1				
19																						1	1	1		
20																							1			
21																										
22																						1			1	
23																						1			1	1
24																										1

The situation was quite different when young animals were considered. The growth rate of animals born during the experimental period cannot be precisely determined since there is no way of knowing the exact age of any animal less than twenty-four hours old. However, the mean length of a large group of such animals should be proportional to the mean age of the group. The mean length of young animals in colonies of each size was calculated for Experiments 1 and 6, and the results are shown in Figure 22. Solitary animals are larger than most
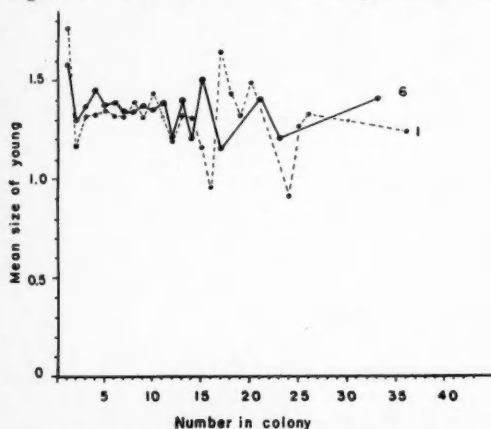

FIG. 22. Relation between the mean size of young *Floscularia conifera* (less than twenty-four hours old) and the total number of animals in the colony at the beginning of the experiment. Solitary animals are given as 1. Solid line, Experiment 6; dotted line, Experiment 1. Size is in micrometer units where $1.0 = 191\mu$.

colonial ones, especially in Experiment 1. The size varies considerably in the larger colonies, largely as a result of the scarcity of such colonies. The mean length of young for all colonies taken together was also determined. In Experiment 1, the mean length of young solitary animals was 338μ, of young colonial ones 267μ. This difference is highly significant according to Fischer's *t* test. Corresponding figures for Experiment 6 are 300μ and 256μ; the difference is smaller but still significant. Evidently, young animals which enter a colony grow more slowly than those which settle alone, but after about twenty-four hours, both grow at the same rate. This may perhaps be explained as an effect of competition for food with adults. The rudimentary corona of the newly attached Floscularia is probably unable to divert much material from the strong ciliary currents set up by the adults, and the animal would not have enough to eat until the corona developed fully.

REPRODUCTIVE RATE

As pointed out before, the reproductive rate of solitary and colonial animals cannot be calculated separately. Further, there is no correlation between the apparent rate of reproduction, or rate of settling, and the standing crop of eggs when different populations are considered. This is shown when the mean

number of eggs in the three experiments is compared with the apparent rates of reproduction. It is probably a result of differences in larval mortality or of emigration on different dates.

Number of eggs

Experiment	Mean for whole population	Mean for animals with eggs only	Reproductive rate
1	0.66	1.57	48 %/day
4	0.14	1.56	18 %/day (?)
6	0.39	1.94	118 %/day

However, within one population, the mean number of eggs in the tube should be a measure of the reproductive rate, since the number depends otherwise only on the rate of development and age. Therefore, the data of Table 10 were broken down to show the length-frequency distributions of solitary and colonial animals classified by the number of eggs in the tube (Table 14). In Experiment 1, colonial animals started laying at a younger age and layed at a faster rate than did solitary individuals. The colonial animals started laying during the second day of life at the rate of 1.5 eggs per day, while solitary individuals started laying almost a day later and layed about 0.77 eggs per day. In Experiment 6 the results were not so sharply marked, although there was a similar tendency for solitary animals to mature and lay more slowly.

LENGTH OF LIFE

The lengths of the tubes of dead *Floscularia conifera* are proportional to the lengths of life, allowing for individual variation in growth rate. Accordingly, the effect of colonial habit on the length of life was studied by computing the mean lengths of tubes of solitary and colonial animals which died during the experiments. Animals which were solitary at the start of the experiment were regarded as solitary even though young may have settled on them during the experiment. This method of computation avoids statistical artifacts due to transfer of animals from one category to the other during the experiment; if it were not adopted much or all of the effect on longevity and the death rate that was observed might be due solely to the fact that the longer an animal lives the greater is the chance of its becoming colonial. The list below shows that animals grew to about twice the length in colonies as they did alone. The difference between mean lengths of living solitary and colonial animals was relatively small.

EXPERIMENT	MEAN LENGTH AT DEATH (μ)	
	Solitary	Colonial
1	802	1604
4	554	1413
6	764	1242

Since there was no significant difference between adult growth rates, this appears to mean that aggregation is very beneficial as it permits longer life. Figure 23 shows the relationship between size of colony and length of life. The increase between solitary animals and colonies of two is very marked.

TABLE 14. Length and age frequency distributions of solitary and colonial *Floscularia conifera* in Experiments 1 and 6, classified by the number of unhatched eggs contained in the tube. The size range is given in micrometer units where $1.0 = 191\mu$. The equivalent age in days of the upper limit of each size interval is given. This table is an extension of Table 10.

Size	Age	Experiment 1 Solitary				Experiment 1 Colonial								Age	Experiment 6 Solitary					Experiment 6 Colonial				
		0	1	2	3	0	1	2	3	4	5	6	7		0	1	2	3	4	0	1	2	3	4
0.0 - 1.0	0.77	10				238								0.59	6					80				
1.1 - 2.0	1.54	416				756	1							1.18	42					328				
2.1 - 3.0	2.31	344	2			531	2	1	1					1.76	51					261	2			
3.1 - 4.0	3.08	147	1			137	2	1	1					2.35	42	4	2			174	15	1		
4.1 - 5.0	3.84	57	10	3		85	12	2	1					2.94	13	13	3	2		48	31	17	1	
5.1 - 6.0	4.61	51	91	17		70	67	14	6	1			1	3.52	2	3	5	4		4	5	21	12	
6.1 - 7.0	5.38	10	45	42	2	21	106	62	11				1	4.12				1		3	2	18	18	3
7.1 - 8.0	6.15	2	8	11		9	72	82	12	1	1		1	4.70		1				6	8	14	17	6
8.1 - 9.0	6.92	1	2	2	1	10	32	75	8	1				5.29		1		1	1	1	1	8	15	2
9.1 - 10.0	7.69		1	1		5	26	56	2	3				5.89		1				1	1	5	1	
10.1 - 11.0	8.45		2	1	1	3	15	34	2	1				6.47							1	3		
11.1 - 12.0	9.23			1		5	7	33	3															
12.1 - 13.0	9.99		1	2			11	11	1															
13.1 - 14.0	10.77					1	8	5																
14.1 - 15.0	11.54	2					8	6																
15.1 - 16.0	12.30					1	3	3																
16.1 - 17.0	13.07						1	2																
17.1 - 18.0	13.84																							
18.1 - 19.0	14.61						1																	
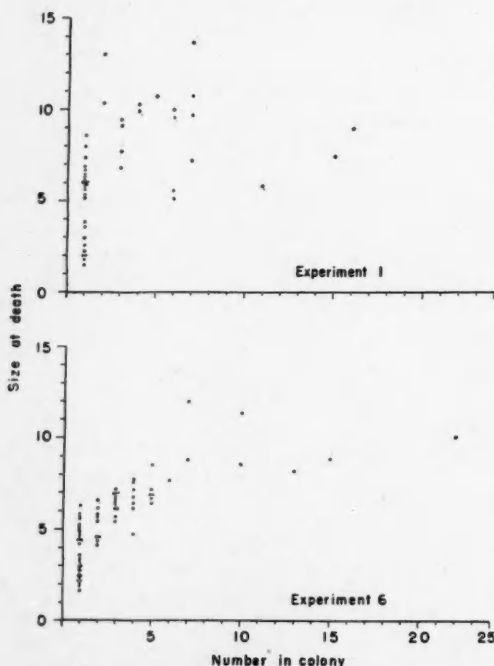
FIG. 23. Relation between size of *Floscularia conifera* at death and number of animals in colony at start of experiment. Each point represents one animal. Size is given as micrometer units where $1.0 = 191\mu$.

Beyond that the increase is small, but regular with increase in colony size in Experiment 6, rather irregular in Experiment 1.

DEATH RATE

The death rate in Experiment 1 was 3% per day for solitary animals, 1% per day for colonial ones. The results for Experiment 6 are listed.

	Solitary	Colonial
First day	9	11
Second day	14	6
Both together	10	8

These results are inconclusive and of doubtful significance, although it seems that the death rate for solitary animals tended to be higher.

The matter was investigated further by calculating the death rates by size classes as shown in Table 15. In both experiments, the death rate was much higher for small solitary animals than for small, colonial animals. In Experiment 6 the rate for colonial animals declined to a point, then increased as if preliminary competition killed off a number of animals, perhaps those with least yolk left at time of attachment; however, one would expect this depression to be more marked in Experiment 1 where suppression of growth was greater. In any case, the minimum in death rate is of doubtful significance. The chief importance of Table 15 is that it shows further that the greater survival in colonies is not a statistical artifact, as discussed in the previous section.

LIFE TABLES

Matters of survival can be studied by means of life tables, which give information on the age distribution of mortality. For discussions of life tables and their significance, papers by Pearl (1940) and Lotka (1934) may be consulted. Pearl & Miner (1935) summarized data on invertebrate animals, and Deevey & Deevey (1944) have given a useful discus-

TABLE 15. Death rates of *Floscularia conifera* as per cent per day, taken over one day in Experiment 1, two days in Experiment 6. Solitary and colonial animals compared by size classes, given in micrometer units where $1.0 = 191\mu$.

Size class	DEATH RATE			
	Experiment 1		Experiment 6	
	Solitary	Colonial	Solitary	Colonial
0.0- 1.0...	0	0	20	8
1.1- 2.0...	1	0	19	6
2.1- 3.0...	0	1	80	0
3.1- 4.0...	2	0	100	22
4.1- 5.0...	3	2	60	24
5.1- 6.0...	10	2	100	52
6.1- 7.0...	11	5	...	72
7.1- 8.0...	25	0		100
8.1- 9.0...	33	6		...
9.1-10.0...	0	11		
10.1-11.0...	0	6		
11.1-12.0...	0	0		
12.1-13.0...	..	6		
13.1-14.0...	..	7		
14.1-15.0...	0	..		
15.1-16.0...	..	..		

TABLE 16. Life tables for *Floscularia conifera* in Experiments 1 and 6, given in terms of the actual numbers of individuals involved. The first column on the left gives the mean size corresponding to the computed age intervals in the second column. Sizes are in micrometer units where $1.0 = 191\mu$. Ages are in days.

d_x' is the number dying at each age.
l_x' is the number surviving at the beginning of each day.
q_x is the death rate each day, d_x' / l_x'.

Mean size	Computed age interval	SOLITARY			COLONIAL			TOTAL		
		d_x'	l_x'	q_x	d_x'	l_x'	q_x	d_x'	l_x'	q_x
					EXPERIMENT 1					
1.3	0-1	1	28	0.036	..	22	0.000	1	50	0.020
2.6	1-2	10	27	0.378	..	22	0.000	10	49	0.204
3.9	2-3	2	17	0.118	1	22	0.045	3	39	0.074
5.2	3-4	0	15	0.000	0	21	0.000	0	36	0.000
6.5	4-5	11	15	0.733	4	21	0.190	15	36	0.417
7.8	5-6	2	4	0.500	5	17	0.294	7	21	0.333
9.1	6-7	1	2	0.500	2	12	0.167	3	14	0.214
10.4	7-8	1	1	1.000	6	10	0.600	7	11	0.637
11.7	8-9	..	..	.....	2	4	0.500	2	4	0.500
13.0	9-10	..	..	.....	1	2	0.500	1	2	0.500
14.5	10-11	..	..	.....	1	1	1.000	1	1	1.000
					EXPERIMENT 6					
1.8	0-1	1	33	0.030	..	42	0.000	1	75	0.013
3.5	1-2	16	32	0.500	..	42	0.000	16	74	0.216
5.2	2-3	13	16	0.812	4	42	0.095	17	58	0.293
7.0	3-4	3	3	1.000	24	38	0.634	27	41	0.658
8.8	4-5	..	..	.....	9	14	0.643	9	14	0.643
10.5	5-6	..	..	.....	3	5	0.600	3	5	0.600
12.2	6-7	..	..	.....	2	2	1.000	2	2	1.000

sion with new data. Ideally, life tables concern a group of animals kept under optimal conditions so that the death rates calculated result from inherent mortality rather than reaction of the population to diverse and varying conditions. Actually this condition is rarely met, and in any case, natural populations live in a variable environment. Bodenheimer's (1938) discussion of physiological and ecological life tables is of interest in this connection.

Records are kept of the age at death of a large group of animals, and these ages ordered chronologically. The chief functions calculated are d_x, the number of animals dying during any stated time interval x, l_x, the number alive at the beginning of the interval, and q_x, the death rate calculated as d_x/l_x. In ordinary demographic practice, a smooth q_x curve is fitted to the data, and l_x and d_x calculated from it. Here, these functions were calculated from the raw data, and therefore are designated by prime signs (l_x', d_x').

Table 16 gives life tables for *Floscularia conifera* in Experiments 1 and 6 in terms of the original data. The d_x' columns are simply frequency distributions of the lengths of animals which died during the experiments. The ages equivalent to the size classes are also given. The l_x' columns were obtained by adding the d_x' columns cumulatively from the bottom. In Table 16, data are given for solitary and colonial animals as well as for the whole population. Unfortunately, the rather long time interval (one day) and small numbers of animals yield rather irregular curves as shown in Figures 24 (l_x') and 25 (d_x'). No attempt was made to fit curves to the data mathematically. In both experiments, there were marked differences between solitary and colonial animals. The death rate of solitary animals was higher, and the l_x' curve therefore is much lower than that for colonial

animals. This was also demonstrated in Table 15. In Experiment 1 the d_x' curve is distinctly bimodal for solitary animals, with no deaths occurring on the fourth day. The curve for colonial animals also has a slight maximum, but this is probably insignificant. Evidently there was great difference between the course of the life of solitary and colonial animals.

In Figure 26, the data have been plotted to permit comparison with three of the four other species of rotifers for which it is possible to calculate life tables.
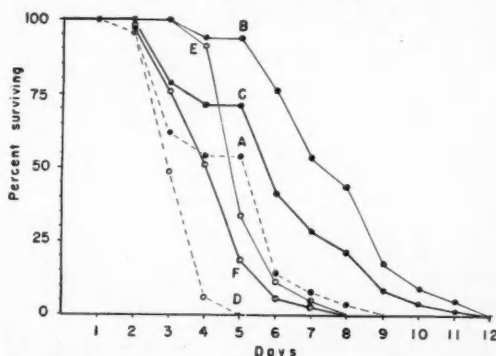

FIG. 24. Survival curves for *Floscularia conifera* in Experiments 1 and 6, giving the percentage of animals surviving at the beginning of the day indicated. Open circles (curves A-C) represent Experiment 6, closed ones (curves D-F) Experiment 1. A and D, solitary animals; B and E, colonial animals; C and F, both taken together.
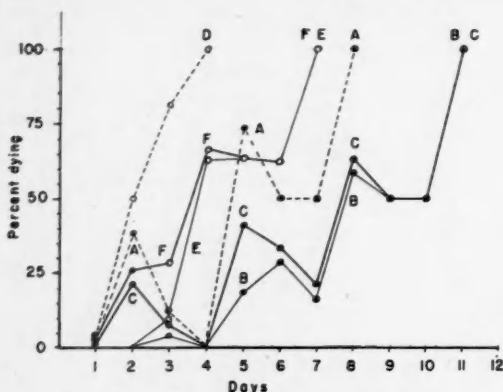
FIG. 25. Per cent of population in Experiments 1 and 6 dying at age represented. Explanation as in Fig. 23.

The ages are expressed as percentage deviations from the mean length of life for each species, where the mean is called 100%, and this subtracted from all other ages (Pearl 1940). The percentage of the original population surviving at various times is shown by the curves. Data for *Proales decipiens* are from Table 39 of Pearl's (1940) book, those for *Proales sordida* were calculated from Table 15 in the paper by Jennings and Lynch (1928), and those for *Lecane inermis* from Table 2 by Miller (1931).
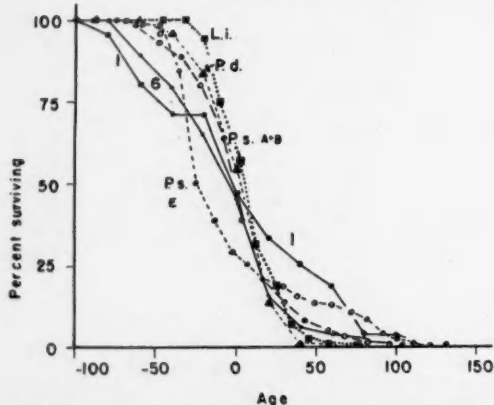

FIG. 26. Survivorship curves (l_x') for *Floscularia conifera* in Experiments 1 and 6 (closed circles, solid line), *Lecane inermis* (L. i., squares, dotted line), *Proales decipiens* (P. d., triangles, dashed line) and two populations of *Proales sordida* (P.s. open circles, dashed lines). Data for *Proales sordida* are from Jennings and Lynch (1928), for *Proales decipiens* from Pearl (1940), for *Lecane inermis* from Miller (1930), and for *Floscularia conifera* from the present paper. The age is given as per cent deviation from the mean length of life which is taken as 100%.

Proales decipiens was shown by Pearl & Doering (1923) to have an l_x curve which approached closely to the extreme rectangular type, but Figure 26 shows that *Lecane inermis* approaches even more closely to

this theoretical type where the animals all live to the same age, then die simultaneously. According to the data presented in Table 6 by Ferris (1932), *Epiphanes senta* also has a more rectangular l_x curve than does *Proales decipiens*, but slightly less so than *Lecane inermis*. The several populations of *Proales sordida studied* by Jennings & Lynch were variable as shown by the two curves for the species in Figure 26. Population "A + B" has an l_x curve much more nearly rectangular than does Population "E" which is more like the intermediate type. The two populations of *Floscularia conifera* studied in the present paper have diagonal l_x curves and thus are quite different from the others shown. It should be remembered, however, that the Floscularia populations occurred under natural conditions while all the other populations were reared in what may be regarded as nearly optimal conditions. It should be pointed out that the comparison made by Jennings & Lynch between *Proales decipiens* and *P. sordida* was based on the length of the life span, and this method gives undue weight to extreme ages where the data are always poorest. The relationship between the curves for the two populations of *P. sordida* is changed greatly when the mean length of life is the basis of comparison. The discussions by Pearl & Miner (1935) and Pearl (1940) are recommended. Apparently the rotifers tend to have more rectangular curves than most other animals.

DISCUSSION

Until the present time, exact work on rates of reproduction, growth, and death rates in natural populations has been limited to certain macroscopic organisms which had special structures or habits that lent them to such study; such as fish by virtue of their scales, or flour or meal organisms which can be kept in the laboratory under conditions which very closely approximate those in nature. It has been necessary to limit growth rate determinations on aquatic microscopic organisms to laboratory cultures which, no matter how carefully controlled and standardized, can hardly represent conditions existing in natural environments. A possible exception is Grim's (1939) work on diatoms in Lake Constance, based on changes with depth and time in the size frequency distribution of the organisms. It is therefore not possible from the studies cited in Table 11 to determine many values necessary for an interpretation of the biocoenosis, for there is no way of knowing just how much growth and reproduction are affected, if at all, by factors which are not controlled in the laboratory experiments. Ecologists are primarily concerned with natural populations, and the extensive laboratory studies, conducted chiefly with a few species of protozoa and insects, usually have at some time had as their stimulus a desire to know more about the intimate workings of natural populations. As Park (1941: 293) writes in discussing the insect work, complex functions of populations can be dissected by laboratory techniques. But it may be noted that even at the very advanced stage which these experimental studies have reached, this really

is dissection, not surgery, and it is not always possible to put the parts back together in a whole which approximates nature, except perhaps in organisms from exceedingly limited habitats.

Therefore, the author feels that it is very desirable to examine every natural population which is capable of any analysis, correlating changes in the various vital rates with environmental changes. As in all such work, the empirical analysis is apt to be inconclusive in some respects and to lack the finesse of the experimental work; however, the empirical approach is of necessity complementary to the experimental one. Thus, not only are the results of interest in themselves, but they should aid in the interpretation of results of laboratory experiments in terms of natural conditions, and so should be of use in consolidating and integrating general knowledge of population dynamics.

As far as the present paper goes, this aspect is given only a rudimentary treatment, for not only are laboratory experiments almost lacking with *Floscularia conifera*, but work on natural populations has only begun. If extensive experiments can be made on the behavior of laboratory populations and their reaction to controlled changes in the environment, and if more experiments can be made with natural populations under a variety of conditions, many aspects of population physiology of these organisms should become clear, with results of considerable interest in comparison with other organisms. The aquatic environment is more complicated and harder to handle experimentally than the air or flour habitats in which so much insect work has been done, and sessile populations may have a specialized physiology; but it is necessary to work with complex situations to understand them, and sessile organisms are by no means an inconsiderable part of the earth's biomass. The successful work of Gause (1928), for instance, with aquatic microscopic organisms shows that careful, quantitative laboratory work of an ecological nature can be done with them.

Another aspect of populations is treated in the present work, and, from the nature of the data, more fully. This is the effect of aggregation. References to and summaries of the extensive literature on this subject can be found in the works by Park (1941), Hammond (1938), and Allee (1931, 1938). It is necessary here only to state that for many species there is an optimal population density at which maximal growth or reproduction, or minimal death, occurs. Many organisms can withstand rigorous environments better in groups than alone, and there are various explanations. The present experiments are of interest for several reasons: the populations occurred in a natural habitat and the aggregations were formed naturally by the animals themselves, and were not held together by force of experimental circumstance. In many experiments with protozoa, the results have been greatly complicated by differential effects of volumetric and density changes on food and experimental organisms, by the possibility of the secretion of stimulative substances by dividing animals, and by other factors inseparable from the technique. Discussions can be found in papers by Hammond (1939) and Richards (1941). In the present experiments, there seems to be no stimulative secretion; the animals were not artifically separated into little groups in glass dishes, for the entire group grew on a plant and occupied a volume of about one liter. Furthermore, there was a definite circulation of water through the pond, so there was little opportunity for localized concentrations of substances unless secreted at a most improbable rate. Nevertheless, aggregation under these circumstances led to spectacular results, for after an initial period of suppressed growth, colonial animals had an expectation of life almost double that of the solitary ones. The initial depression may very likely be an effect of competition for food, but the author has been unable to think of a reasonable explanation, on the basis of present data, for the effect on surivival. Possibly, given a certain minimum of food, the rotifers are incapable of growing faster than a certain rate, but the greater ease of getting food with mutually reinforced water currents may permit longer survival, although this does not seem likely. It is remarkable that the effect of aggregation is shown almost as strongly by two animals as by greater numbers. Experiments designed to solve this problem evidently need concern primarily only the differences between solitary and pairs of animals. There is no clear evidence of an optimal concentration of animals since mean growth rate is the same in both large and small colonies, and survival in large colonies did not appear to be definitely less than in smaller ones, although it is suggested by Experiment 1.

The relationship between the population and its substrate has been given considerable attention, both in Part I and the present paper. This may be relatively simple in many situations, as the fouling of piles or the periphyton of sticks or other non-growing substrates where the course of events is determined mainly by the character of the population itself. But populations on such plants as Utricularia are subject to modification by the fact that part of the substrate is constantly disappearing or being made unsuitable while new parts are being formed; this imposes an obligation to keep moving. Certain organisms cannot maintain themselves in quantity on such a substrate because they do not possess motile stages, or the motile stages do not migrate far enough and in sufficient quantity. The relative rarity of Bryozoa and perhaps sessile diatoms on Utricularia, observed during this work, may be a result of this. Observations in the Bird Preserve Pond suggest that *Floscularia conifera* makes larger colonies on the relatively permanent Typha than on Utricularia. A Utricularia plant with its associated periphyton can be considered a dynamic unit with all parts exhibiting distal extension. Any given association may be in a state of population inequilibrium if, by some chance, a group of slowly extending animals attach, for this group would be in process of being lost. A relatively slight immigration, however, might serve to maintain such animals on the plant in small numbers. Changes of the growth rate of the plant may

modify the attached population by separating animals or permitting heavier concentrations. Graded variations of the chemical nature of the surface may accentuate such effects, as *Collotheca gracilipes* is presumably affected by the development of pectins on the plant cells (Edmondson 1944).

To return finally to the topic with which Part I opened, consider the use of the terms periphyton, epiphyton, and lasion. Periphyton is the totality of attached organisms on a substrate, and can be further designated as epiphyton or lasion depending on whether the organisms are simply scattered on the substrate and are not associated mechanically, or whether they form a more or less dense growth and the individuals are associated mechanically and are interdependent. Roll (1939) gave a full discussion of the history of the terms. This is a common sort of definition in biology which is usually indefinite because the terms are descriptive of an evenly graded development; actually no distinct separation can be made. Roll gives two figures which admirably exemplify the definitions of epiphyton and lasion, but it is difficult to know just what to call a periphyton which consists of a few scattered filaments of Bulbochaete, each with a rich coating of attached diatoms and protozoa. The situation is complicated by the dynamic, changing character of the periphyton. A lasion no doubt starts as an epiphyton, developing by growth and reproduction of primary settlers and secondary immigrants through a series of changes to the point where constituent organisms can no longer behave as if they were alone on the substrate, but are subject to all favorable and harmful effects of crowding by the rest of the population. It is reasonable to examine the terminology of the periphyton from a dynamic viewpoint in order to see if the terms can be useful in discussions of sessile organisms.

The Bulbochaete periphyton mentioned can represent the problem, since it is a common type of periphyton. The author knows of no specific work on the effects of crowding in this genus, but the effects of crowding are so well known for a great variety of organisms, although chiefly animal (Allee 1931, 1938), that it is fairly safe to assume that crowding has harmful and beneficial results, and that an optimal density exists. In any case, social effects certainly exist for so many of the animal members of the periphyton that the discussion which follows is generally valid.

If there are energetic or other physiological relationships between the organisms which vary with the density in a non linear manner, relatively small variations in density may have large effects on the population. Thus a developing periphyton may start with a scattering of Bulbochaete with a concentration so low that there are no social effects and each plant grows as if it were alone on the substrate. But with an increase in density, there might begin reciprocal relationships between the plants which result in increased growth and reproduction. With this change, the relationships among attached diatoms and protozoa might be changed. With further growth, passing optimal concentration, there would begin to be depressive effects on the Bulbochaete which might be either accentuated or alleviated by the diatoms.

The optimal concentration of any major constituent of the periphyton may of course be changed by presence of other organisms in quantity, and in a periphyton consisting of several major species, the relationships would become very complex. A curve could be drawn, for simpler situations anyway, showing the relation between population density and growth or reproduction or length of life; e.g., Allee (1934: Figs. 13, 19, 20). This curve would rise with increasing density to a maximum, have a more or less flattened top, then decrease. Evidently the first point of inflection represents the concentration where wholly beneficial effects of aggregation are beginning to be offset by harmful effects. This point could be chosen to separate epiphyton from lasion. On the other hand, the point at which the effect is maximal might be chosen, since it represents the density at which beneficial effects overweigh deleterious ones to the greatest extent. The important point is that even if there is a smooth morphological or density transition in the development of a sessile population from one extreme to another, the associated effect on the physiology of constituent organisms need not be smooth. If it were, the two terms under consideration would not be very useful. There is evidence in the present work to show that at least in some sessile animals, the effect is not smooth.

The effect of crowding on *Floscularia conifera* is marked in that it enhances survival by about 100%. Whether two animals standing side by side would have the same effect as when one is attached to the other is not known but needs to be investigated. Figure 23 shows that density of the Floscularia population, as measured by colony size, has a marked effect on survival; two animals together survive much longer than two alone, while three survive still longer. There is a vague suggestion of an optimal colony size in Experiment 1, but in Experiment 6 a concentration high enough to decrease survival by a significant amount was evidently not found. It is difficult to express colony size and density on substrate in comparable terms, but it is quite evident that at some degree of propinquity, the animals begin to affect each other. Such relationships should be sought out and examined carefully, for it may be that during the development of a lasion, there is a point at which there is a more or less sudden change in the course of events following the attainment of a critical density. That this can be a low density is shown by the fact that the effect on survival in Floscularia is almost as great for two as for five.

In most natural situations, relationships are greatly complicated by the fact that interspecific competition and other effects between species operate to an important degree. This is very well shown in the rather diagrammatic figures and the discussion given by Ivlev (1933). There, for instance, on glass slides suspended in water, a large population of sessile protozoa develops, but is completely crowded off by

filamentous algae. When the algae have finished their life cycle and die off, the protozoa return in quantity. Evidently there is a concentration of algae above which sessile protozoa are not able to find sufficient space for attachment and feeding. The effect of environmental factors in effectively keeping the populations in a young, undeveloped state is shown in the same paper, where the effect of water velocity, by keeping out some organisms and modifying the growth of others, is demonstrated. This paper substantiates in a general way the foregoing speculations as to the possible course of events in an algal periphyton.

These matters have been considered at some length here to show that a real problem exists that is not merely one of terminology, but is of some significance in the dynamics of sessile populations. It must be realized when terms that describe divisions of the periphyton are defined, the dynamic state of a population probably cannot be determined merely by looking at it. If the terms are to be based on dynamic definitions they cannot be merely descriptive of appearance, although an obviously sparse population is more likely to be an epiphyton than an obviously dense one. This does not imply that such terms cannot be useful, for by making the language of ecology fit the conditions more closely, we can discuss the principles of ecology in a more economical and understanding manner.

SUMMARY

1. Of the four species of sessile Rotatoria studied on *Utricularia vulgaris americana* in the Yale Bird Preserve Pond, each had, when abundant, a maximum concentration characteristically placed along the axis of the plant; well toward the proximal end for *Floscularia conifera*, *Ptygura longicornis bispicata* and *Beauchampia crucigera*, very near the distal for *Collotheca gracilipes*. The latter species probably reacts to the chemical nature of the leaves, while *Floscularia conifera* may react to the amount of minute periphyton.

2. Each species appears fairly early in the summer, builds up to a maximum abundance, and declines toward autumn. *Floscularia conifera* apparently does not grow or reproduce at temperatures below 10° C. as judged by laboratory experiments.

3. A method is described for marking the tips of the tubes of all *Floscularia conifera* at a definite time in such a way that subsequent rates of growth, apparent reproduction or settling and death can be determined. This method disturbs the environment to a very slight degree. Six experiments were performed of which three give usable quantitative information. *Ptygura longicornis bispicata* and *Beauchampia crucigera* can also be studied this way.

4. The mean growth rate of *Floscularia conifera* varied from 153μ to 334μ per day. The rate of settling, or apparent reproduction varied from 18% per day to 125% per day. Death rates varied from 2% per day to 9% per day in the three experiments in which it could be measured, but it was probably much higher in Experiment 2.

5. The form of the population, or quantitative distribution along a plant depends on the reproductive rate of the rotifer, its rate of migration, and the growth rate of the plant. If rates of reproduction and substrate growth are equal, the rotifer species with the highest rate of migration distally will have its population maximum furthest distal. A lower rate of reproduction implies a less conspicuous population maximum, as does an increased rate of substrate growth. The Utricularia plant with its associated fauna may be regarded as a dynamic unit, with all parts exhibiting forward extension. The results of interaction of the variables mentioned are apparently comparable to the situation described briefly by Burkenroad for the epiphytic fauna of pelagic Sargassum, and are probably of general applicability.

6. The actual rate of reproduction, or rate of egg production, was estimated from length frequency distribution of animals classified according to the number of unhatched eggs in the tube. It was 181% per day in Experiment 1 and 169% per day in Experiment 6. This gives as estimates of embryonic and larval mortality 73% and 14% per day respectively. Part of this may be accountable to variable migration from the plant. The length of the period of immaturity was between 1.5 and 2.0 days in both experiments. The mean length of the embryonic period was about 3.8 and 2.4 days in Experiments 1 and 6 respectively. These results are compared with those for other species in laboratory populations.

7. Length frequency distributions of *Floscularia conifera* suggest that there are marked variations in the rate of reproduction, but that these are not diurnal.

8. Considerable attention is given to the effect of aggregation on *Floscularia conifera* and the intensity of colony formation. After a period of initial depression in growth rate of young entering a colony, solitary and colonial animals grow at the same rate, but the expectation of life for colonial animals is about double that of solitary animals. The reproductive rate is less in solitary animals, which start laying about a day later than those in colonies. The death rate is much higher for small solitary animals than for small, colonial animals.

9. Life tables, based on all animals which died during Experiments 1 and 6, were constructed and compared graphically with three other species of rotifers, *Proales decipiens*, *P. sordida*, and *Lecane inermis*.

10. Attention is directed toward the terminology of the periphyton and the necessity for considering the dynamic as well as the morphological structure.

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THE BIRD POPULATION OF AN ELM-MAPLE FOREST WITH SPECIAL REFERENCE TO ASPECTION, TERRITORIALISM, AND COACTIONS*

ARTHUR C. TWOMEY

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THE BIRD POPULATION OF AN ELM-MAPLE FOREST WITH SPECIAL REFERENCE TO ASPECTION, TERRITORIALISM, AND COACTIONS

INTRODUCTION

Biologists recognize that both animals and plants are important in all communities and constitute an inseparable unit in their structure. Throughout the world, both vertebrate and invertebrate animals belong to various major plant and animal communities which include deserts, prairies, coniferous and deciduous forests, etc. Ecologists call these largest plant-animal communities "biomes" or "biotic formations." They are divided into "associations" which include some wide-ranging species among the dominants and important influents; these constitute the elements of unity in the climax portions of the biome. The associations are interrupted by seral stages which, under natural conditions, develop toward the climax.

Some of the earlier workers perceived distinct "habitat" preferences among birds. Judd (1902) propounded "habitat" preferences and associated them under the following headings: birds that nest in the open fields, birds that depend on covers, birds of less limited distribution and birds of varied distribution. He made no correlations as to the relationships of birds within a given locality but stated that there was a "habitat" preference among the birds of a limited farm area in Maryland which he had studied. Another early paper that discussed this preference in detail was that of Forbes (1907). By his bird census, taken across the corn-belt of central Illinois in early autumn, he pointed out the existence of a feeding ground preference which was influenced by the dominant crops in the area covered—corn, pasture and stubble. Forbes was able to determine statistically the preference for different crops and the aggregation of species in them. Adams (1908) was one of the first to evaluate the position of birds within a biotic community. His correlations were drawn from a grouping of the birds according to plant succession. There was no discussion of the birds from the standpoint of community relationships. Pitelka (1941) illustrates the coincidence of biotic communities with bird distribution. This is the first attempt to develop this viewpoint and offers the ornithologist an alternative to the life zone concept.

There are numerous individual life histories recorded in the literature, but little attention has been given to the interaction of birds with other members of a community. Williams (1936), in a report on a beech-maple climax community, demonstrated that avian populations are a factor in community dynamics. The present study presents further evidence confirming this thesis. During the past fifteen years several investigations have been carried on in an elm-maple forest (the William Trelease Woods, formerly University Woods, five miles northeast of Urbana)

that belongs to the University of Illinois. The previous researches determined the characteristic species which make up the animal community in such a forest, and included a record of their life-habits and a study of their environment as it affected their existence. McDougall (1922) grouped the plants of this forest according to their significance. Weese (1924) made a study of the animals during 1921-1922. Blake's analyses of the 1924-1925 winter population of the animals was published in 1926. In 1925-1926, Smith (Davidson) (1928) studied the climax and developmental stages of the forest. Blake (1931) made a comparison of the 1924-1925 animal communities with those described by Smith (Davidson) and Weese. In the meantime Smith-Davidson (1930) reported on the tree-layer society and, later, on the effect of seasonal variation of weather upon the population of animals in the succession of a deciduous forest. Rice (1939) and Kanatzar (1935) studied the invertebrate population for the periods 1933-1935 and 1935-1936, respectively. From 1938-1940, Koestner (1939) studied the mammals of Trelease Woods. He writes that his actual catches for 1938-1939 totaled 54 fox squirrels and 43 rabbits, and for 1939-1940, 65 squirrels and 73 rabbits. Lindeborg (1941) observed the fluctuation in abundance of Peromyscus and Blarina in Trelease Woods. During the fall of 1937 and 1938 he noted a sharp increase that dropped off during the spring of each year.

Observations begun by the author in 1933 at the Trelease Woods are being continued indefinitely as a research program, or until enough data have been accumulated to give significant and accurate indication of the population trends. The writer's investigations continued from the fall of 1933 until June of 1936. For uniformity of comparison, however, only 1934 and 1935 are herein considered.

DESCRIPTION OF COMMUNITY STUDIED

Trelease Woods, located in the park-land region of east central Illinois, covers approximately 22 hectares with about 20 hectares of actual forest. The county

topograpical map shows the 690- and 706-foot contour lines passing through the woods. There is a difference in level between the highest and lowest points of about 16 feet, which gives a slightly rolling aspect.

The soil is the yellow-gray silt loam characteristic of upland forest, the limits of which are but little beyond the present border of the woods to the north and east (Hopkins *et al.* 1918). The drainage in the forest is poor because of the slight slope and impervious subsoil. In the early spring the low spots are always filled with water or are extremely moist. If rain is abundant, the water may stand for several weeks. Thus, throughout a wet season, the forest floor is saturated with moisture, and during the entire year the low ground remains moist. The distribution of the vegetation reflects variation in soil moisture as shown by the more dense growth in the sub-climax areas. The nearest stream is a tributary of the Salt Fork (of the Vermilion River), which flows eastward about four hundred yards south of the forest.

The area lies within the red oak-maple ecotone between the beech-maple and oak-hickory associations. The map of the woods made by McDougall (1922) shows only 13 per cent of the plots without maple trees. At the present time, however, even these contain many sizable maple seedlings. In view of these facts, and for convenience of general discussion, the entire woods will be treated as climax. The division of the woods into climax and late sub-climax portions is clearly illustrated on the map (Fig. 1) and is further substantiated by the breeding areas selected by the different species of birds (Fig. 6). The plant constituents have been described by McDougall (1922) and by Marberry, *et al.* (1936). Of the total tree population, approximately 29 per cent is sugar maple (*Acer saccharum* Marshall) and 22 per cent is American elm (*Ulmus americana* L.) and red elm (*Ulmus fulva* Michx.). Red oak (*Quercus borealis* Michx. var. *maxima* Ashe) is prominent in the climax portion. Other trees found in the woods are the white or American ash (*Fraxinus americana* L.) the blue ash (*F. quadrangulata* Michx.), the basswood or American linden (*Tilia americana* L.) and the blue beech (*Carpinus caroliniana* Walt.). There are occasional trees of other species sparsely scattered throughout.

The shrubs are not uniformly distributed. They are densest on the intermediate ground between the high and low places. There is a long strip of shrubs along the west side extending inward 25 to 45 meters. This strip varies in width; across the north end, it is 24 to 30 meters wide, while at the southern edge, it widens from 45 to 90 meters, probably on account of light conditions. The prevalent shrub is the pawpaw (*Asimina triloba* Dunal), which usually grows from one to three meters but sometimes attains a height of ten meters. The spice bush (*Lindera benzoin* (L.) Blume), which varies from one to two meters in height, is second in abundance. The remaining shrub-sized plants are largely tree seedlings.
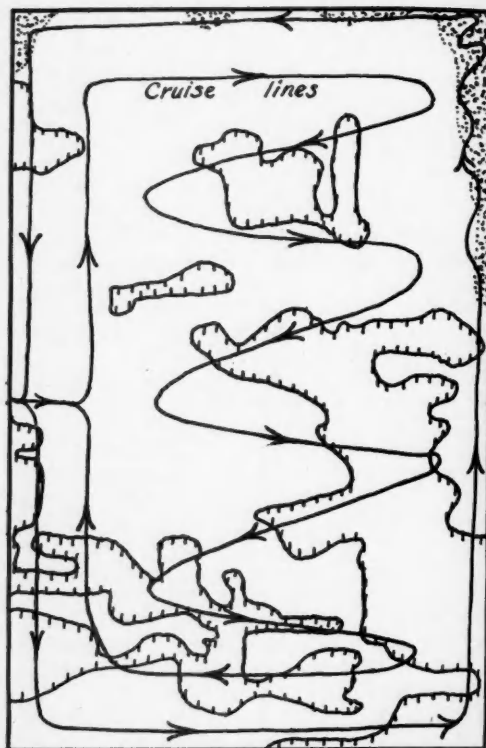
FIG. 1. Climax areas and cruising routes. The lines pointing inward mark the red oak-maple climax. Stippling shows unwooded areas. The remainder of the area is late sub-climax. Cruising route is indicated by line with arrows.

The herb seasonal groups are vernal, aestival and serotinal. The wild-ginger (*Asarum reflexum* Bickn.) and the water leaf (*Hydrophyllum canadense* L. and *H. appendiculatum* Michx.) flower in spring but remain green for the remainder of the summer and wilt after the killing frosts. The dutchman's breeches (*Dicentra cucullaria* (L.) Bernh.), spring beauty (*Claytonia virginica* L.), jack-in-the-pulpit (*Arisaema atrorubens* (ait.) Bl.) and many others are also characteristic vernal plants. During the aestival and serotinal periods the wood nettle (*Laportea canadensis* (L.) Gaud.) is very abundant, often attaining a height of over four feet. It occurs in dense groupings, which may cover almost a hectare. At this time of the year other common herbs are the touch-me-nots (*Impatiens pallida* Nutt. and *I. biflora* Walt.).

Four to six centimeters of decaying leaves and other debris cover the moist ground layer of the forest floor. According to Weese (1924) this area was heavily pastured previous to 1918; some of the hardwoods (*Juglans nigra* L.) were cut *circa* 1895. For about 22 years the forest has remained undisturbed, and the woody plants have almost come back to their normal conditions.

The area studied is completely surrounded by cultivated fields, and the nearest woods is one-fourth mile to the southwest and a half mile south. As a result of this isolation, agricultural and prairie insects are abundant in the woods (Metcalf & Flint 1939) and maintain a much more important position in the community than they would in a larger natural unit.

METHODS OF STUDY

OBSERVATION

Motile animals, whether invertebrate or vertebrate, are difficult to observe, chiefly because of their movements, and different methods must be used for the various groups. For this research, the following system was adopted:

1. Careful estimations of the bird populations were made twice each week throughout the period of study, both for the forest and forest edge. The forest edge is defined as that area in which seedlings, shrubs, vines and herbs form a dense cover at the margin of the main forest—reaching neither into nor out of the forest proper more than 60 meters.

The observer entered the main west gate (Fig. 1) and walked east 60 meters into the woods. He then walked north along the west, and east along the north side, but kept within 60 meters of the edge of the woods or the inner margin of the shrub strip. A general southward path was next followed, crossing and recrossing the woods at least six times until a point 60 meters from the south edge was reached. A path along the south side was taken to within 60 meters of the west edge and along the west side to the gate. This completed the forest observations. For the forest edge, the center path was followed with deviations into the forest edge as far as 30 meters. The general direction followed was again from the main gate but south along the west edge and across the south end, up the east side with an irregular route along the margin of the north half of the east edge, then across the north end and down the west side to the gate. This procedure was carried out each time a census was taken. Several checks were made throughout the study when classes of 25 to 30 students cruised the woods, and the numbers of birds noted on these trips compared favorably with the author's counts.

It was necessary to employ a more nearly detailed method for estimating numbers of migratory individuals. A complete census of the forest edge was always made, but for the forest proper, a sampling plan was used. For instance, at each census a plot (30 meters square) was chosen in some part of the woods and a careful count made of all birds within this area. Similarly, additional plots were selected far enough away so that the observer's earlier activities did not interfere with the movements of the birds. These counts served as a basis for the calculation of the numbers present in the whole forest.

The main winter population was found along the east forest edge and was sometimes difficult to count accurately because the flocks kept moving out in front as the observer proceeded through the woods. In order to take a census, the observer walked along the east edge, starting at the southeast corner, and worked steadily northward. As the northeast corner was approached, the birds that had been moving ahead flushed from cover at the north end. They would then fly up and move back south, passing overhead. Thus the individual members of each species were easily ascertained.

2. Observations in the forest were not always made at the same hour of day. Conditions were studied at sunrise, noon, afternoon, and evening. Likewise, observations were made during heavy rains and snows to determine whether or not the animals would react differently under these more severe weather conditions.

3. During the summer residence of the birds, from May to September, observations were made nearly every day.

4. Emphasis was placed on special phases of animal activities; birds were studied while they were feeding, incubating or carrying on territorial activities.

5. A close watch was kept for any sign of the presence of predators.

6. Specimens were taken for stomach analyses.

METEOROLOGICAL RECORDS

As an aid in the study of the animals of the elm-maple community, meteorological records (including soil and air temperatures and relative humidity) were kept. The instruments for recording these data were enclosed in a standard weather bureau type instrument shelter, located about 30 meters in from the west forest edge in the north portion of quadrat 76 (McDougall 1922: 204). The instruments were at the level of the low shrub stratum.

A recording hygrothermograph was used to obtain records of the air temperature and relative humidity. The humidity readings were checked weekly with a sling psychrometer. Standard maximum-minimum thermometers were used as a check upon the accuracy of the hygrothermograph.

A soil thermograph also was located within the shelter box and continuously recorded the temperature at a two-inch depth in the soil. The sensitive element was placed just underneath the surface of the soil, which was covered with leaf mat and other debris.

From the records made, monthly means were computed and used in the correlation of movements of vertebrate and invertebrate populations with weather conditions.

It was necessary to obtain other weather data from the records of the Urbana Station of the United States Weather Bureau, located on the campus of the University of Illinois, Urbana, Illinois. Inasmuch as any existing differences between the altitude of the two locations, or the exposure at the two stations were not great enough to introduce any appreciable variation between the means of the Urbana

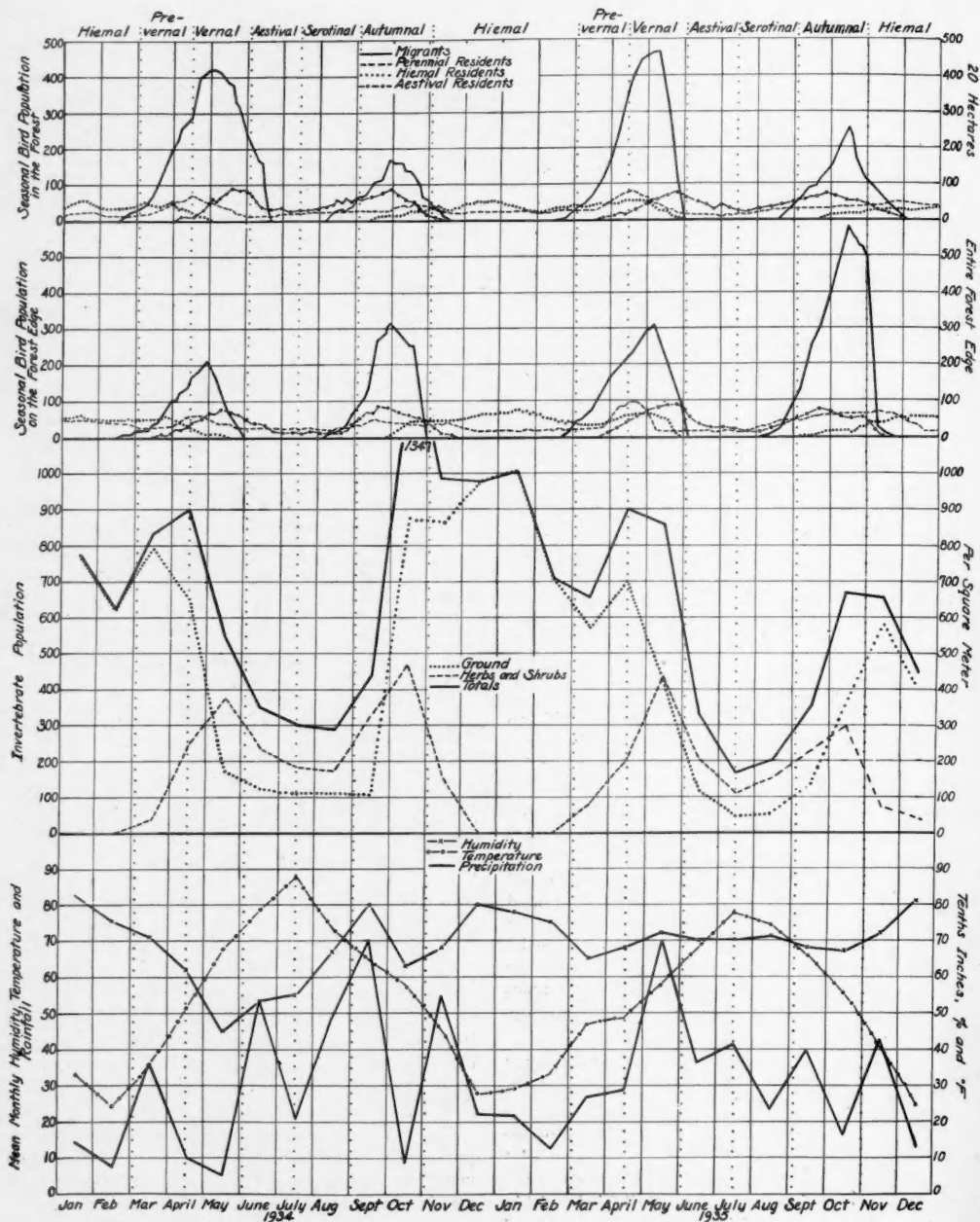FIG. 2. Correlation of bird and insect populations with seasons and weather. From top to bottom: seasonal populations of the migrants, aestival, hiemal, and perennial residents estimated separately for forest and forest edge; total insect population, total number of insects on shrubs, and in soil; precipitation in inches of rain per month; mean monthly temperature in degrees F, and mean monthly per cent humidity.

Station and those of the woods station, temperature averages and other data of the Urbana station were assumed to be equivalent to those of the woods station.

CLIMATOLOGICAL DATA

The hiemal and perennial avian populations exhibited fluctuations from season to season, especially on account of local movements. In order to interpret these changes correctly, weather data were carefully examined. In most cases the local movements of a species of bird are governed by the direction of the prevailing winds and, in part, by the available food supply. In those instances in which the food of the particular species of bird is largely insects, it is necessary to evaluate weather conditions which cause the fluctuations in available insect population. These weather factors are: air and soil temperatures, relative humidity, precipitation and the direction of prevailing winds. Comparisons of seasonal differences in the invertebrate and bird populations and monthly means for the years involved are presented in tabular and graphic form (Fig. 2, Table 1).

ASPECTION

The biotic seasons are characterized by a decline to a minimum of individuals of one seasonal group and the beginning of the appearance of another. In seasonal community study, biotic seasons are referred to as hiemal, prevernal, vernal, aestival, serotinal, and autumnal aspects (Weaver & Clements (1929); McDougall (1931); Clements & Shelford (1939)). Smith (Davidson) (1928) used these terms in describing seasonal communities in a deciduous forest succession. The latter diagrammatically depicted the more common invertebrates in the various societies. Birds were mentioned in the seasonals, but only the

junco and the tree sparrow were listed as belonging to the hiemal society. Smith-Davidson (1932) also pointed out the abundance of certain spiders which occurred during various biotic seasons.

The use of the biotic seasonal groupings was found to be of value in discussing the activities of birds; along with insects and other invertebrates, they appear to follow the pattern of the seasonal phenomena of any given locality, although the dates vary from locality to locality and from year to year. The following dates are typical of the elm-maple forest for 1934 and 1935.

Hiemal Aspect...........November 1 to March 1
Prevernal Aspect..............March 1 to April 15
Vernal Aspect..................April 15 to June 1
Aestival Aspect.................June 1 to July 15
Serotinal Aspect...........July 15 to September 1
Autumnal Aspect......September 1 to November 1

HIEMAL ASPECT

This period is one of cold winds, snow and rain. It is a season of minimum bird population, made up of the tree sparrow, slate-colored junco, brown creeper, red-tailed hawk, and perennial residents. Although the insects are in hibernation, some display a certain degree of activity, especially on warm days when they come to the surface of the ground stratum. This insect activity is responsible in part for the erratic movement of the hiemal residents (Fig. 2, Table 1). Throughout the hiemal period the avian population remains fairly uniform, although there is a noticeable increase during the latter part of the period (February) because of population movement from the surrounding areas coincident with the start of the insect migration from beneath the leaves of the ground stratum.

TABLE 1 A. Fluctuations in bird populations. Totals per month. Young birds are counted as soon as independent of parents.

1934	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
Humidity, Relative	81.3	77.2	72.1	61.6	46.8	56.5	57.3	69.7	80.5	55.5	73.3	51.5
Mean Temperature, °F.	32.5	24.6	35.4	53.2	70.5	60.8	83.5	74.9	64.5	57.9	65.7	27.8
Migrants: Forest	....	30	50	375	400	150	....	25	140	130	50	
Migrants: Forest Edge	....	20	50	200	150	10	....	40	350	375	20	
Permanent Residents: Forest	20	18	30	50	40	20	20	25	30	40	35	30
Permanent Residents: Forest Edge	50	45	30	55	50	30	30	30	50	45	45	35
Summer Seasonals	....	....	....	....	....	156	156					
Winter Seasonals: Forest	50	45	40	35	10	....	....	....	15	30	35	40
Winter Seasonals: Forest Edge	50	40	40	50	25	....	....	....	....	30	40	50
TOTAL POPULATION	170	198	340	765	675	366	206	120	585	660	225	155
1935												
Humidity, Relative	77.1	76.6	74.6	69.0	73.3	70.5	70.3	70.5	70.4	76.1	78.7	79.7
Mean Temperature, °F.	29.0	32.9	46.4	50.1	58.1	69.4	79.1	74.8	67.3	53.7	40.1	24.9
Migrants: Forest	....	30	100	450	350	350	....	50	100	250	75	
Migrants: Forest Edge	....	20	175	320	200	....	....	150	425	450	50	
Permanent Residents: Forest	30	30	35	60	40	20	18	30	30	30	40	30
Permanent Residents: Forest Edge	20	30	35	100	20	20	20	50	50	60	60	25
Summer Seasonals	....	....	....	....	....	136	136					
Winter Seasonals: Forest	30	30	30	40	20	....	....	....	10	20	30	30
Winter Seasonals: Forest Edge	55	50	40	50	30	....	....	....	15	25	50	50
TOTAL POPULATION	135	190	415	1020	630	523	174	230	630	835	305	135

Prevailing wind direction exerts an influence on the hiemal bird population in that the winds are principally from the north and northwest. The birds seeking the more sheltered localities are invariably found scattered over the east and south forest edges and often 40 or 50 meters back into the forest. Hiemal residents are absent from the middle of May until the middle of August.

PREVERNAL ASPECT

The appearance of numerous early Diptera and various beetles marks the beginning of the prevernal period. Leafhoppers and other hibernating insects come to the surface and begin their vertical movement into the shrubs; increasing numbers of robins scratch over the duff of the forest floor in search of adult and larval insects; bluebirds begin to catch flies; tufted titmice and cardinals commence calling; woodpeckers start their drumming; and the first northward migratory birds, the most prominent of which are the fox sparrow, golden-crowned kinglet, crow, cowbird and hermit thrush, begin filtering in. Toward the end of the prevernal period, there is a definite impetus in the activity of the birds as they begin pouring in from the south. Green shoots sprout up through the drab cover of dead leaves, new buds are bursting, and the insects have moved into the shrubs and have started to migrate toward the edge of the forest.

VERNAL ASPECT

The vernal aspect is one of intense activity. Dutchman's breeches (*Dicentra cucullaria* (L.) Bernh.) and spring beauty (*Claytonia virginica* L.) are scattered in profusion over the forest floor. The new foliage of the shrubs and trees soon covers the forest. A host of seasonal birds swell the forest population to its maximum numbers (Table 1, Fig. 1) and simultaneously, the greatest number of insects appear. Warblers are everywhere; sparrows seek the dense

tangle of the forest edge for food or shelter from hawks. These seasonals appear in the following diminishing order of abundance: white-throated sparrow, ruby-crowned kinglet, myrtle warbler, yellow-bellied sapsucker, Cooper hawk, Tennessee warbler, chipping sparrow, warbling vireo, Baltimore oriole, yellow warbler, Cape May warbler, prothonotary warbler. Many of the perennial birds are building nests. The vernal period ends with the passage of the northward migrants and the last movements of the agricultural and prairie hibernating insects out of the forest.

AESTIVAL ASPECT

An abundance of nesting birds characterizes the aestival period. The indigo bunting, red-eyed vireo, crested flycatcher and wood pewee establish territories. The period changes from one of song to silence as the feeding of the nestlings takes more and more of the adults' time. Spiders as well as numerous flies that are not found at other times of the year are abundant in the herb and shrub stratum. Weese (1924) designates this period by a decrease in the total invertebrate population due to the absence of migratory insect forms.

SEROTINAL ASPECT

The young birds leave their nests, almost *en masse*, marking the opening of the serotinal period. The territories are no longer retained, and the birds travel in family groups. The cardinal, tufted titmouse, red-headed woodpecker, downy woodpecker, red-eyed vireo, crested flycatcher, and wood thrush wander throughout the forest. In August a dispersal into the surrounding areas (beyond the area under discussion) causes a sudden decrease in the avian population, a serotinal phenomenon (Fig. 2, 3). By late August the first migrants from the north, the blackburnian warblers, appear but spend most of their time in the forest. These are followed by the main warbler mi-

Seasonal movements within layer societies

	PREVERNAL				VERNAL				AESTIVAL				SEROTINAL				AUTUMNAL				HIEMAL			
	GS	HS	C	TT	GS	HS	C	TT	GS	HS	C	TT	GS	HS	C	TT	GS	HS	C	TT	GS	HS	C	TT
CARDINAL																								
INDIGO BUNTING																								
MARYLAND YELLOW-THROAT																								
WOOD THRUSH																								
RED-EYED VIREO																								
WOOD PEWEE																								
DOWNY WOODPECKER																								
RED-HEADED WOODPECKER																								
WHITE-BREASTED NUTHATCH																								
TUFTED TITMOUSE																								
STARLING																								
BARRED OWL																								
YELLOW-BILLED CUCKOO																								
RUBY-THROATED HUMMINGBIRD																								
CRESTED FLYCATCHER																								

GS = GROUND-LOW SHRUB SOCIETY   HS = HIGH SHRUB SOCIETY
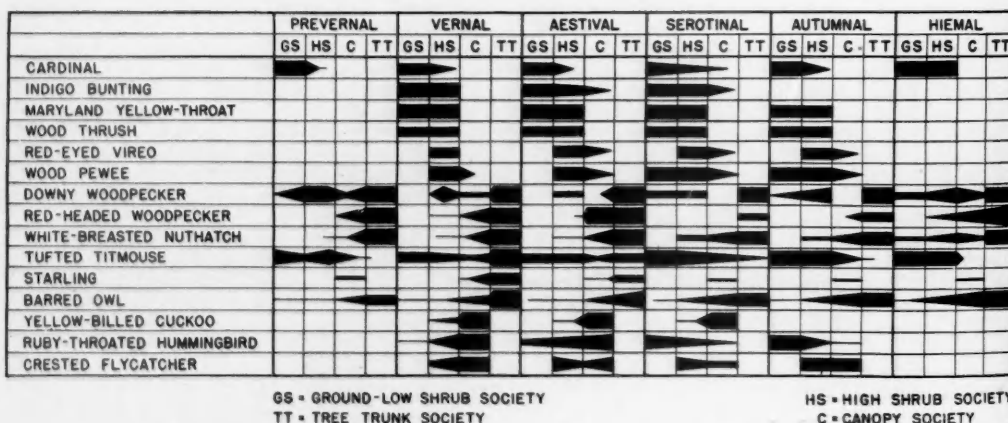TT = TREE TRUNK SOCIETY   C = CANOPY SOCIETY

FIG. 3. Seasonal movements within the layer societies. The width of the black area is based on the relative time spent by each species in the layer societies throughout the various aspects.

gration. The summer residents disappear. The numbers of southward migrating birds gradually increase. Weese (1924) found that many additional insect types, the lantern-flies, *Acanalonia conica, Ormenis pruinosa,* and *Ormenis septentrionalis,* appeared in the herb stratum during this period.

AUTUMNAL ASPECT

The most striking phenomenon of the autumnal period is that of movement both in the insects and birds. The daily range of temperature, particularly the sudden fall of night temperatures and the shortening of the daylight hours, is no doubt partly responsible for the increased activity. The forest margin and agricultural invertebrates move inward from the forest edge and downward to the forest floor (Weese, 1924). The sudden jump in the avian southward seasonals to a maximum number in late September and early October occurs as waves of these birds meet the insect maximum on the forest edge (Fig. 2). The abundance of weed seeds and fruits on the forest edge at this time also plays an important role in causing this concentration. During both years, 1934 and 1935, the autumnal migration reached its height during the last week of September and then fell off rapidly.

The following list of seasonal birds includes the most abundant and common species in the order of their appearance from September 1 to October 1: blackburnian warbler, Tennessee warbler, black-poll warbler, warbling vireo, slate-colored junco, tree sparrow, fox sparrow, ruby-crowned kinglet, song sparrow, hermit thrush, white-throated sparrow, rusty blackbird, robin, olive-backed thrush, gray-cheeked thrush.

DISCUSSION OF ASPECTION

The elm-maple community in the deciduous forest area is broken into distinct seasonal aspects. The movements and appearance of groups of birds and insects tend to be correlated with the seasonal variations of the plant matrix. The general avian population, a highly specialized and mobile group, exerts a pressure from coaction that changes with the biotic seasons. The seasonal or migratory birds take an enormous toll of the various invertebrates that characterize the aspects. This influence is greatest during the vernal and autumnal periods. The birds that remain in the community as summer residents are principally insectivorous and require great numbers of insects for food during the aestival aspect and an even greater abundance during the serotinal period because of young birds. The returning seasonals are in part late serotinal, but principally autumnal. With the rapid expansion in the seasonals during the autumnal aspect, there is a corresponding increase in the insect populations, as well as the appearance of seeds and fruits. Many of the birds at this season reverse their food habits wholly or in part by eating seeds and fruits instead of a completely insectivorous diet. The perennial avian population is relatively stable in numbers and species. Their role in coaction is easily absorbed within the community under normal circumstances. The minimum of activity is during the hiemal aspect when only the perennials and hiemal avian residents are present.

AVIAN POPULATIONS

The term population implies a known number of identified individuals living in an area. All biological censusing strives to approach this implied ideal. In the case of nesting birds, investigators make use of the observable phenomena of mating, of nest building, and of the feeding of the young, to identify individuals. The writer believes that, for the nesting season, he has arrived at the number of birds of each nesting species, and thereby the total number of birds in the woods, with a good degree of accuracy.

However, outside the nesting period where a type of strip cruising was employed no claims of accuracy can be made. The identity of individuals is entirely obscure and thus no real knowledge of the character and magnitude of the population is obtainable by this method. Color banding or other method of marking individuals was not used because it is far beyond the capacity of a single investigator, or perhaps of many investigators, when applied to such an extensive area.

Suggestions of the deficiencies of the method may be seen in the increases and decreases in populations which are evident. For example, the permanent residents show concurrent increases and decreases in the forest and forest edge, suggesting for the migration period that individuals of the species are present as "permanent" residents, but some additional individuals migrate into the area while en route north and thus increase the total. It further suggests for other periods that there is migration to and from adjacent woodlands, etc. Further comparison of the forest and forest edge numbers suggests rapid movement from one to the other during the counting process so that the same individuals may have been counted more than once, but there is no way to ascertain how many individuals are counted twice or more. The writer does not know how many of the individuals counted had regular or permanent headquarters in the woods under consideration, how many were out visiting other areas, or how many were visiting in the area of study from nearby woods. During the migration period it was not possible to know which individuals are en route as distinguished from those that stay throughout the year. The counts are concerned only with individuals recognized as belonging to a particular species. The writer is convinced however that the figures obtained constitute a reliable index of a population probably somewhat smaller than the figures indicate.

SEASONAL CHANGES IN AVIAN POPULATION

Fluctuations in population of the various aspects are demonstrated (Figs. 2, 3) for 1934 and 1935. The shifting population of the forest is compared diagrammatically with special reference to seasonals, hiemal residents, aestival residents, and perennial residents. There is a noticeable fluctuation in the bi-weekly average number of birds.
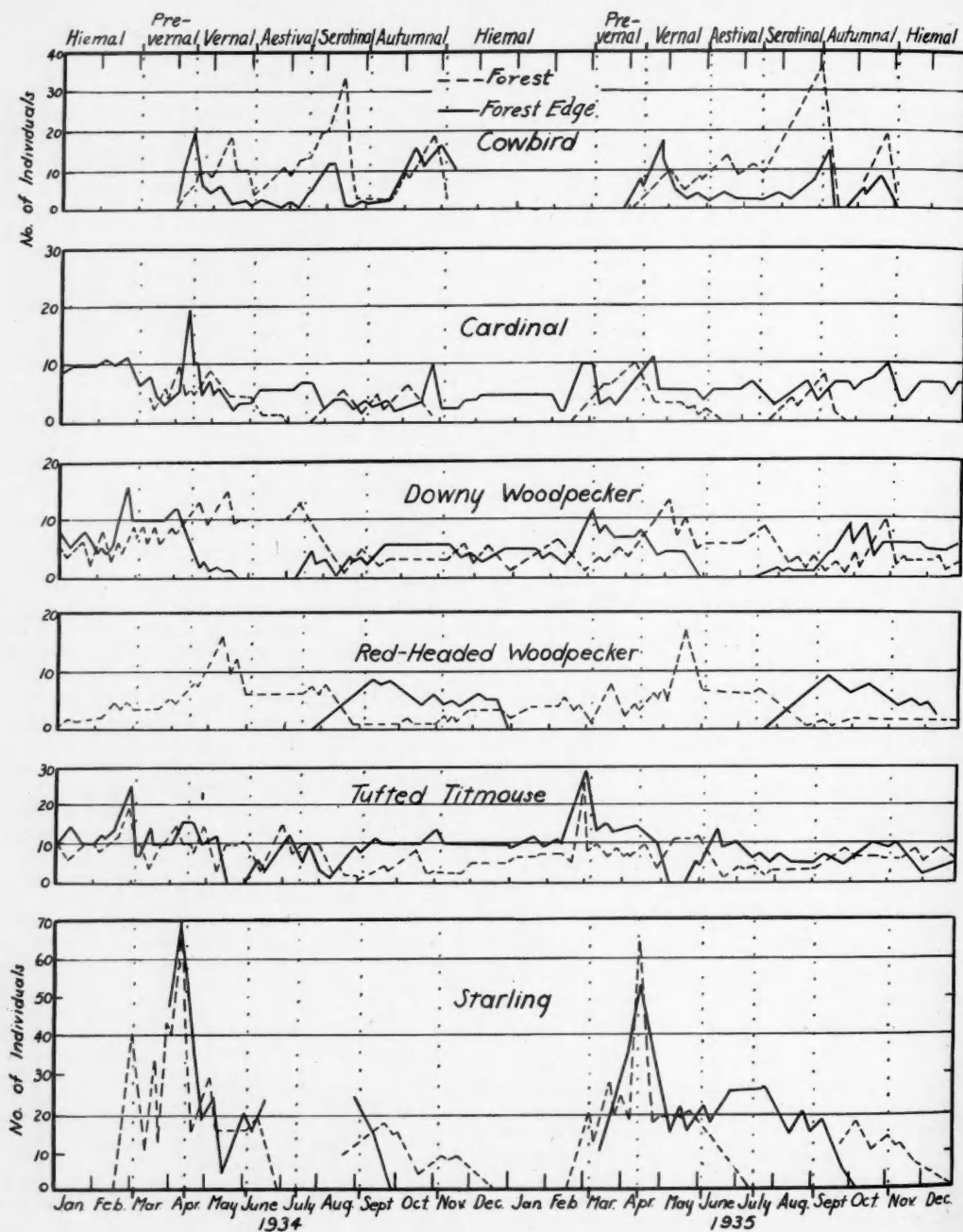
FIG. 4. Number of birds using the forest and forest edge throughout the year. Some birds evidently moved back and forth between forest and forest edge while the count was being made and are included more than once in the number recorded. Preferences for the two different kinds of cover are indicated. This and the following figure show primarily that certain species are forest-edge birds part of the year and forest birds the remainder; at certain seasons, the whole population wanders over the forest and forest edge, depending upon the weather, food, cover, etc. Broken line shows numbers observed in the forest. Solid line forest edge.

The variations in the seasonal bird population, apparent even among the perennial residents, are fairly uniform for the two years. Young birds brought about an augmentation in the nesting population during the vernal and serotinal aspects, but in the span of a year, through dispersal and general mortality, this increase is not discernible in the returning population. The charts (Figs. 3, 4) of forest-edge and forest populations were made primarily to show that certain species are forest-edge birds part of the year and belong to the forest during the remainder; while at certain seasons, the whole population wanders over the forest and forest edge, depending upon the weather, food, cover, etc. Thus in the individual species charts, part of the population may be on the edge one day and in the forest the next. Thus the charts cannot be used to determine the total population by simply adding the forest and forest-edge figures. For instance in a wintering population tree sparrows are forest-edge birds while tufted titmice are found both on the forest and forest edge.

Permanent residents are not a stable population in the woods, but have periods of fluctuation in numbers, particularly during time of increase due to young birds. During the hiemal minimum there is increased activity because of lower temperatures and subsequent wandering throughout the forest in search of food. Permanent residents are made up of birds that are both forest and forest-edge dwellers and, as a result, the total population curve for the permanent residents tends to be approximately the same for both the forest and forest edge.

Variation in the total annual population, as well as fluctuation in the various aspects from year to year, is bound to occur so that conclusions based on only two years must be evaluated with a consideration for the specific local factors as they affect the community. An analysis of Table 1, and Figure 2 shows that the vernal peaks for the seasonals are greater in the forest than on the forest edge both in 1934 and 1935.

Two graphs incorporated into Figure 2 show the total monthly precipitation and the mean monthly temperatures. There was a total precipitation of 35.15 inches in 1934 and 37.21 inches in 1935. The daily mean temperature for a 24-hour period is obtained by applying the formula:

$$\frac{7 \text{ A.M.} + 2 \text{ P.M.} + 2 \times 7 \text{ P.M.}}{4}$$

Vernal migration peaks were reached at 65° F. in 1934 and at 61° F. in 1935. Smith (1917), who carried on observations from 1903 to 1922 in the same general locality, declares that the greatest migratory activity in spring occurred at times when the weather maps showed areas of low barometric pressures approaching from the West, with the south winds and rising temperatures which normally accompany them.

The abundance of insects and birds may be correlated with the occurrence of rain and subsequent plant growth during the vernal and aestival aspects. These two periods of 1934 were dry. In 1935 the heaviest rain for the year fell in May; from June to the first weeks of August, frequent rains also were

TABLE 1 B.   Number of pairs of breeding birds.
* permanent residents.

	1934	1935
Cooper Hawk...............	0	1
Mourning dove.............	0	2
Yellow-billed Cuckoo........	2	1
Barred Owl*...............	1	1
Hummingbird..............	1	1
Flicker...................	1	1
Red-headed Woodpecker.....	4	2
Hairy Woodpecker*.........	1	1
Downy Woodpecker*........	5	4
Crested Flycatcher.........	5	4
Wood Pewee..............	3	4
Crow*...................	2	5
Tufted Titmouse*..........	5	4
White-breasted Nuthatch*....	1	0
House Wren..:............	3	4
Catbird..................	1	1
Brown Thrasher...........	1	1
Wood Thrush..............	3	3
Starling..................	8	10
Red-eyed Vireo............	8	4
Yellow-throat.............	2	1
Cardinal*.................	3	3
Indigo Bunting............	22	21
Goldfinch.................	2	..
Field Sparrow.............	2	2
Song Sparrow.............	1	1
TOTAL (excluding cowbird)...	87	82

recorded. This produced a luxuriant plant growth that in turn afforded a more adequate cover within the community and a subsequent enlargement of the general food supply.

Insects affect the local and seasonal movements of the bird population to a pronounced degree, but insects are at the same time physiologically controlled by the precise climatic and biotic seasonal phenomena that stimulate the physiological mechanism of the birds. The biotic balance of excess populations is apparent throughout the period of observation. The birds (seasonals, aestival residents, hiemal residents and perennials) follow the pattern of aspection. A rise in temperature during the hiemal period brings many insects out of hibernation, and in response the birds shift their feeding territories to the area of greatest food abundance. Another example of this balance is illustrated by the sharp advance in the sparrow and warbler population and the prevalence of small predatory hawks during the vernal and hiemal migration periods. Figure 2 shows that the general insect populations of the soil, herb and shrub stratums shift during the various aspects (Rice, ms.). The graph is based on sweepings of shrubs and herbs, $1m^2$ for each sweeping, and the population of the soil invertebrates was determined on those taken on a $0.1m^2$ area. The specimens were collected by the sampling method over the entire forest. Soil samples in December, January, February, and March show the abundance of hibernating species and also indicate a seasonal population change that corresponds to the general insect movements. During the remainder of the year, after the emergence of the winter populations, the soil contains a fairly constant

number. A comparison of the two years shows a relatively uniform population and consistent seasonal movements. The 1935 herb and shrub population is much larger than in 1934. This increase accompanies the more luxuriant herb growth in 1935, caused by the wetter vernal and aestival periods.

Weese (1924) emphasizes the marked biotic seasonal coordination of the community components: "The most striking phenomena of the entire period covered by the collections were the hibernating reactions of the autumn, involving a migration inward from the forest margin and downward to the forest floor and the migration in the opposite sense in the spring. The principal inciting factors of the former seemed to be the fall in temperature and the great daily range of temperature of the early autumnal period. The latter was likewise a response to the changing temperature conditions of the forest, supplemented, perhaps, by changing moisture and light conditions. The fact that many species react alike and at the same time to the same stimulus or combination of stimuli shows a great degree of similar adjustment to the climatic rhythm of the temperate savannah on the part of the characteristic insects of the region."

SEASONAL MOVEMENTS

In addition to the seasonal changes of bird populations caused by long migrations, there are local, seasonal movements that illustrate the importance of species within the community. These movements, especially between forest and forest edge, agree with the correlations already made in relation to general insect oscillations and avian population movements. The following observations of the most abundant species in the elm-maple forest are evaluated as to their seasonal societies within the community.

The cardinal (*Richmondena cardinalis cardinalis*) can be found almost entirely along the forest edge (Fig. 3) where there is an abundance of food—seeds, berries and insects. From October to the middle of November there is a tendency toward redistribution, for the birds travel from one wooded section to another. By the first week of December they become more settled and remain comparatively so for the remainder of the winter. With the advent of the prevernal aspect in March, cardinals are noted in the forest proper as often as on the forest edge. In the vernal period they are found on the forest edge, but as the nesting period advances, they move into the dense cover just inside the edge and into the forest proper. Here they begin nidification, and from then until the first of August they are, for the most part, forest inhabitants. During the period of feeding the young, the cardinals are on the ground a great deal. A large percentage of their food consists of midge larvae, pentatomids, numerous beetles and lepidopterous larvae secured from the ground and low shrub layer. During the latter part of July there is a slight rise in the cardinal population, but by August a drop occurs. Until after the fall migration, they range over the entire forest and forest edge. Then, from late serotinal and on throughout the hiemal and

prevernal periods, they again become forest-edge dwellers.

The spring migration of the indigo bunting (*Passerina cyanea*) starts during the first week of May and reaches its peak about May 20 or a little later (Fig. 5). Although primarily a forest bird at this time, a few (mostly males) frequent the forest edge. During the peak, flocks of 10 to 25 buntings are found on the forest floor—generally in the dense underbrush. By the first week of June the numbers decrease and the majority of those that remain become forest-edge inhabitants. A sudden gain in the population (due to the appearance of young birds) takes place from July 10 to 30, but after the first week of August there is a dispersal of the young to the surrounding areas, although the adults are still common throughout August. In 1934, however, nests with young which may have been second broods were found as late as August 15 to 18. They disappear early in September on their autumnal migration.

Upon arrival in the elm-maple forest in early May, the Maryland yellow-throat (*Geothlypis trichas trichas*) is very shy and difficult to approach. Although never abundant in the community, almost continuous singing shows their presence. During the spring and fall migrations, as many as twelve individuals were recorded. Only two pairs in 1934 and one pair in 1935 nested on the forest edge. Throughout their entire summer residence, from early vernal to the late autumnal aspects, these birds are forest-edge inhabitants, seeking a feeding ground as well as concealment for themselves and their nests in the heaviest tangle of the ground-low shrub society.

The wood thrush (*Hylocichla mustelina*) begins to arrive during the first week of May (Fig. 5) and is distributed over the whole forest. By early June, when the thrush migration reaches its peak, the birds show a preference for the forest edge where they can secure an abundance of food. In a few days, however, there is a decided change in their habitat preference. The males begin to sing, and the mated pairs choose definite territories along the west side of the forest—about 60 meters in from the forest edge. Three pairs selected nesting sites at intervals of 150 meters (Fig. 6, No. A) in an area of abundant pawpaw and spice bush, where they remained and confined their feeding activities throughout the aestival aspect. Between July 20 and 28, there was a gain (due to young birds) followed by a drop with the shifting of the new population into other woods. Near the end of August the migration of individuals from farther north was responsible for a steady rise in population which reached the autumnal migration peak by mid-September.

The red-eyed vireo (*Vireo olivaceus*) appears in small numbers throughout the forest during the first week of May (Fig. 5). By May 10 the birds move into the forest, and, except for an occasional hunt for food on the forest edge, they remain almost entirely in the forest proper. They feed on leaf-hoppers, midges, lepidopterous larvae, lacewings and numerous other insects in the dense lower shrub layer
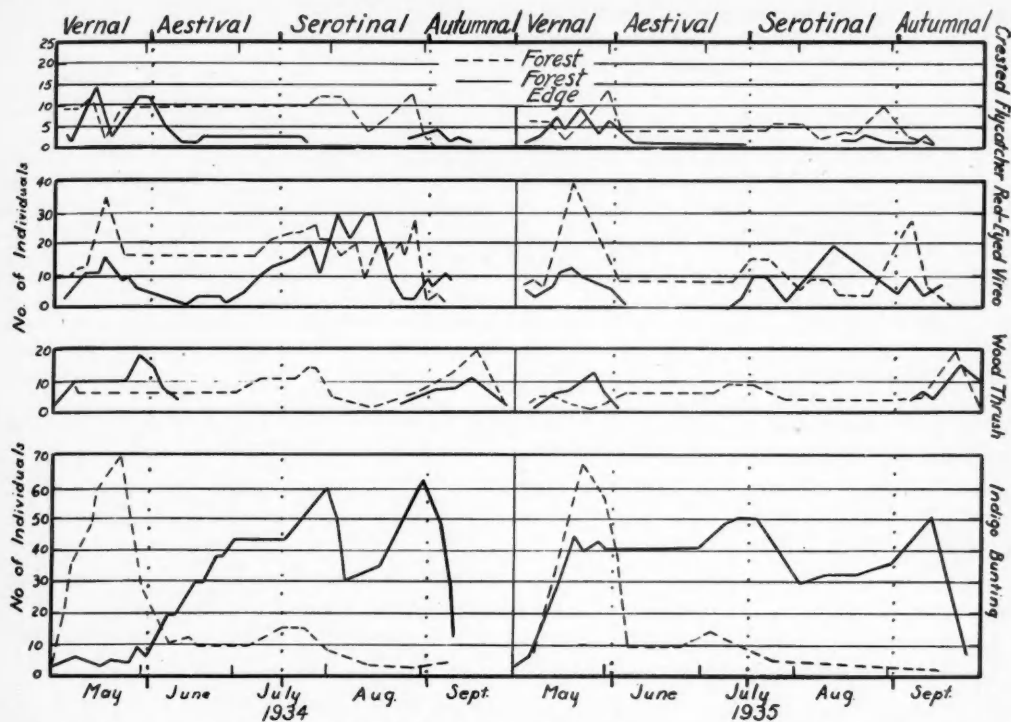
FIG. 5.   Number of birds using the forest and forest edge throughout the year. From top to bottom: crested flycatcher, red-eyed vireo, wood thrush, and indigo bunting. For further description, see Fig. 4.
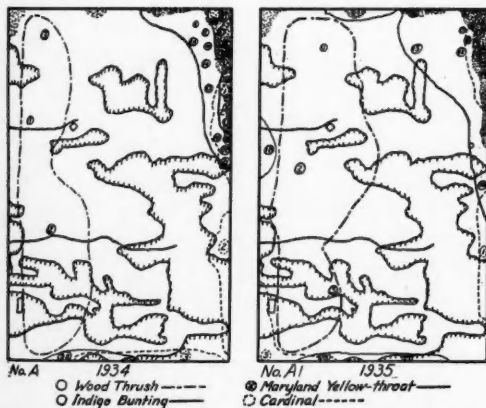
FIG. 6.   Nests and territories. Ground-low shrub society. A, 1934; A₁, 1935. Lines pointing inward mark the climax communities of the forest. Irregularities of the forest edge are indicated by stippling.

and up in the forest canopy. By the end of July they again become wanderers and frequent the forest edge as much as the forest. During the first week of September, the vireos are found chiefly in the forest, where their food is in greatest abundance, and finally, by the middle of September, they begin their southward migration.

Except for the warmer days, the downy woodpecker (*Dryobates pubescens medianus*) is a forest-edge dweller throughout the greater part of the hiemal period (Fig. 4). A change in movements begins about the last week of February, and by the first of March, there is a high peak caused by the transfer of scattered winter populations into the woods. From the latter part of the prevernal period, the birds remain on the forest edge in fairly constant numbers. About the first of May the woodpeckers become forest dwellers. Mating occurs and the pairs establish territories. Young birds augment the population during the later vernal interval, and all remain strictly forest inhabitants until the middle of the aestival period when there is a general dispersal into outlying areas.

The tufted titmouse (*Baeolophus bicolor*) is generally regarded as a forest-edge bird (Fig. 4). With the approach of winter, the population drops to about half because of dispersion to other localities. Throughout the hiemal period this bird spreads out over the whole forest. From May to the middle of June, it remains almost entirely in the forest, where pairs build their nests and raise their young in old woodpecker holes. From the middle of June throughout July, the young birds travel about with the parents, both in the forest and on the edge, in search of food. After the breeding season in late spring, the titmice become seclusive, and the singing becomes less vigorous and frequent as the summer progresses. This

concurs with the findings of Gillespie (1930), who says that, throughout the late spring, summer and early fall, titmice tend to disappear, denoting a period of retirement during nesting and subsequent molt.

The starling *(Sturnus vulgaris vulgaris)* leaves the forest in September, becoming very gregarious throughout the hiemal aspect. During this period large flocks fly over the cultivated fields and feed on grain and ground beetles, as shown by stomach analyses. On bright sunny days the few individuals that remain in the forest occupy branches of some tall dead tree, where they sun themselves and imitate songs of native birds and calls of barnyard fowls. They spend the colder days and cold nights in the hay-lofts of neighboring barns. As March approaches, more starlings appear in the forest. The largest concentrations coincide with sudden drops of temperature. These spasmodic changes in temperature seem to be a stimulus for intense breeding activity which usually lasts for about two days. Then only the breeding pairs remain in the forest. After the eggs are laid, few starlings are seen either in the forest or on the edge (Fig. 4). From the middle of May until the first week of June, they spend the greater part of their time going from the forest to the nearby fields for food. When the young are able to fly (about June 20), the birds move to the forest edge; by the middle of August almost all go into the open fields.

From the middle of December until the first week of July, the red-headed woodpecker *(Melanerpes erythrocephalus)* seldom is seen outside of the forest (Fig. 4). The winter population includes but three or four individuals. In May, additional birds move in from outlying wintering territories. With the approach of the breeding and nesting season in June, there is another slump in the population. By July, when the young appear, there is an increase, and, at the same time, a movement toward the forest edge. This movement is due to a change in their feeding coactions, for now the woodpeckers could be seen flying from some favorite telephone pole, fence-post or dead tree, catching insects on the wing. At this time the young, although almost fully grown, are fed prodigiously by the parents. From then until the middle of December, the woodpeckers become wanderers and are found in the forest, at the forest edge, and also at a distance from wooded areas. After December 15 they move into the forest, and the winter population becomes established.

The white-breasted nuthatch *(Sitta carolinensis carolinensis)* is a permanent resident of the forest and spends most of its time creeping over the trunks and branches of the larger trees. In 1934 two pairs spent the winter in the woods, but in 1935 only one pair was observed. As the prevernal period approached, the nuthatches became more active and one or two additional males appeared. The breeding period terminated with only one pair choosing a nesting site. Their activities were restricted to a limited area in the woods (Fig. 8, No. C). By the early

aestival period, the young left the nest and roamed throughout the forest with the adults. The family group of five individuals stayed together until the late autumnal period, when the young left the woods. The adults remained and established their hiemal quarters.

The crested flycatcher *(Myiarchus crinitus boreus)* appears during the first week of May (Fig. 5). The birds wander extensively over the forest and spend much of the time far up in the heavy forest canopy on the forest edge. They also come close to the ground on the lower shrubs, where they are able to catch the abundant flying insects. As the nesting period progresses, the flycatchers gradually become less numerous on the forest edge, and for the remainder of their stay, they are found almost exclusively in the high canopy of the forest proper. The birds leave the forest and begin their autumnal migration during the last week of August.

During the first week of June, the yellow-billed cuckoo *(Coccyzus americanus americanus)* arrives, usually in pairs, and immediately occupies the forest canopy. In 1934 two pairs nested in the woods, while only one pair was present in 1935. They are strictly summer residents and leave the forest early in September. Throughout their residence, they restrict their activities to the forest and its canopy and are never seen on the lower forest edge.

As the autumnal period approaches, the cowbird *(Molothrus ater ater)* is noticed more on the forest edge; some are seen in the forest but do not feed there to any great extent (Fig.4). Toward the middle of October there is a rise in population that lasts about ten days and is due to the autumnal migration. The cowbirds practically vanish from the forest by the end of October. They are not observed from the middle of November to the first week of April, but the vernal migration brings a wave of cowbirds that follow the movements of the insects from the forest to the forest edge. From May to August cowbirds are scarce on the forest edge. The breeding population (15 to 20 individuals) travels throughout the forest in bands of three or four females with one or two males. By the middle of June young birds begin to add to their numbers. The increase continues until August, when there is a slump as the immatures and adults move from the forest to the open corn fields and pastures. For the next two months few cowbirds are seen in the forest, but as the autumnal migration wave approaches, many birds occupy the tall trees of the forest edge.

DISCUSSION OF SEASONAL MOVEMENTS

The individual species may be divided into two distinct groups—perennial residents and summer visitors. The perennial residents, such as the cardinal, downy woodpecker and red-headed woodpecker, show a seasonal preference for either the forest or the forest edge (Fig. 4). The downy and red-headed woodpeckers are usually regarded as forest inhabitants, but during the serotinal, autumnal and early hiemal periods, the red-headed woodpecker ranges out to the forest edge. The downy woodpecker, un-

like the red-headed woodpecker, is a wanderer. Consequently it is found as much on the forest edge as in the forest, except during the breeding season, vernal and aestival periods, when it is almost wholly confined to the forest. The tufted titmouse is even a greater wanderer than the downy woodpecker, yet it remains in the seclusion of the forest during the vernal nesting period. The cardinal, a forest-edge bird, enters the forest during the vernal and aestival periods. The starlings are distinctive in relation to the movements of the other perennial residents in that they occur irregularly both in the forest and forest edge throughout the year. They are forest dwellers during their nesting season from March to June, but continue to move outside for food. In early April the appearance of large numbers of starlings in the forest after a rapid drop in temperature, demonstrates the effectiveness of sudden temperature changes upon the breeding activities of the species.

The second class of birds consists of summer residents—all of which are migratory. The crested flycatcher, red-eyed vireo and wood thrush, which are, for the greater part of their residence, forest inhabitants, display a preference for the forest edge during the vernal and early autumnal periods (Fig. 5). The indigo bunting, primarily a forest-edge bird, exhibits a preference for the forest during the vernal period, and some individuals even remain in the forest to nest. The cowbird is more of a wanderer over the whole forest and forest edge, especially during the nesting period (Fig. 4).

The seasonal movements of the birds are comparatively consistent for both 1934 and 1935. There are no broad deviations, although slight fluctuations in numbers of individuals do occur. Specific species respond, in general, to similar seasonal environmental variations.

TERRITORY

The term "territory," as used in this study, is in agreement with the use of the term as defined by Howard (1920), Palmgren (1932), Lack & Lambert (1933), Mayr (1935), Tinbergen (1939), Crawford (1939), Noble (1939), and Nice (1941). These investigators all regard this avian activity from the standpoint of an individual species rather than as a community phenomenon. Howard (1920) discusses territory in relation to reproduction, warfare between species, and defense of chosen sites. Noble (1939) gives the most simple and straightforward explanation, ". . . territory is any defended area. . . ." To explain the varied and intricate complex of avian behavior, Nice (1941) distinguishes six types of territory which deviate slightly from those proposed by Mayr (1935) : mating, nesting and feeding ground for young; mating and nesting, but not feeding ground; mating station only; territory restricted to narrow surroundings of nest; winter territories; and roosting territories. The present study indicates that these designations are not rigid and are subject to modifications that depend upon the particular species in question with regard to locality, community pref-

erence, and aspection. Individual species within the community are considered in relation to their particular habitats and territorial preferences throughout the various aspects of a community. In its broad sense, then, territory may be defined as a seasonal community phenomenon which tends to bring the influx of an avian population into the aspects of a biotic community. Not only is there a seasonal change or aspection in the deciduous forest biotic community, but the forest is stratified into distinct layer societies that follow the seasonal change of the plant matrix and animal influents. Birds, highly specialized influents of the community, belong to one or more layer societies, that depend upon the seasonal aspect (Fig. 2).

In the following detailed discussion of territories, the birds of the elm-maple forest are grouped under (a) ground-low shrub society—cardinal, wood thrush, Maryland yellow-throat, indigo bunting; (b) high shrub society—red-eyed vireo, wood pewee; (c) tree trunk society—downy woodpecker, red-headed woodpecker, white-breasted nuthatch, tufted titmouse, starling, barred owl; (d) upper canopy society—yellow-billed cuckoo, ruby-throated hummingbird, crested flycatcher. These categories are based on the choice of the nesting site of the particular species at a time of relative stability within the community.

GROUND-LOW SHRUB SOCIETY

The birds in this society are inhabitants of the dense undergrowth both in the forest and on the forest edge. Here they establish territories, build nests and continually search for food, gleaning insects, snails, etc., from the foliage or scratching for larvae among the debris of the forest floor. Their territories are well defined and overlap very little. Few other nesting species except the cowbird and tufted titmouse penetrate into this society.

The cardinal *(Richmondena cardinalis cardinalis)*, a perennial resident in the forest and forest edge, formed a winter range which served as a common feeding ground on the east forest edge and inward for a distance of 30 meters. By the end of the hiemal period in February, the males began to sing, and there was a general intensification of activity. From this time until the vernal period in May when they began to breed, the birds moved into the forest for short intervals, probably because of the insects coming out of hibernation. As the prevernal period ended and the vernal commenced, the males sang continuously. It soon became apparent that individual males were singing from one locality, and the females were building nests in the same areas. At this early establishment of the territories around the singing posts, the males became aggressive and drove the sparrows, buntings and warblers away from their immediate territories. The nesting territories extended into the forest on an average of only 3 meters, but they followed along its length for distances of 60 to 90 meters. The birds showed no tendency to wander beyond their established territories and consequently there was no interference with other cardinals. After the hatching of the young, a preference

for the forest edge was indicated (Fig. 6, Nos. A, A1). The young left the nests by the middle of June, and this circumstance prevented conflict in the territories with later nesting birds such as the indigo bunting. The territories were abandoned quickly, and there was a shift of the population into the forest. Again in the late serotinal period, the cardinals returned to the forest edge, while the young left the vicinity.

The wood thrush *(Hylocichla mustelina)* arrived in May, in small migratory flocks which never exceeded 10 individuals, and moved about over the whole forest, showing no preference for any particular part. As the aestival period approached, there was a change in activity, and those individuals that chose to nest farther north moved on. At first the songs of the males were heard from various parts of the forest. Then as June advanced, territories were established, and individuals were heard singing more consistently from one locality. In the meantime, the females began the construction of the nests, while males alternately sang and aided. The location of the nests is plotted in Figure 6, No. A. There was never a sign of overlapping of the extremities in the range of any two pairs within the strip of forest undergrowth that constituted the individual territories, and they chose approximately the same territories both years. As the young began to hatch, the adults were more active and traveled in all directions in search of food. After the young left the nests, the males retained their old singing positions. A dispersal of the young out of the forest was noticed in August. Only a few individuals remained until the late serotinal and early autumnal periods, when the migrants began to move into the forest. As during the vernal migration, this interval was characterized by a general wandering over the whole forest. The greater abundance of insects in the undergrowth of the forest edge made it even a greater attraction at this time than during the spring migration.

The Maryland yellow-throat *(Geothlypis trichas trichas),* strictly a forest-edge bird, was found only along the east side of the woods. Because of the wary habits of the birds, it was difficult to observe their activities minutely. Throughout May there was little indication that they had chosen territories. Males sang continually, but not always from the same localities. They shifted as the migrants passed through the woods. By the first of June the two remaining pairs had chosen nesting sites. The song of the male was used as an index of an established territory. Each was located on the forest edge and was separated by at least 40 meters. The actual boundaries were not well defined until the young were being fed, when it could be seen that the territories were marked out by the limits of the feeding ranges (Fig. 6, No. A1). These territories overlapped those of the indigo bunting and cardinal, but there was never any evidence of competition between the nesting species. In no case, however, would the buntings, yellow-throats or cardinals tolerate a close approach of another bird to their nests. Thus there was a dis-

tinction between the territory and the nesting site among the members of the ground-low shrub society. After the young left the nest (first week of July), they stayed with the adults as family groups during the remainder of the aestival and throughout the major portion of the serotinal period. Nesting territories were abandoned on the arrival of the first migrants in late August, and at that time family groups could not be differentiated. The migrants, as well as the resident birds and their young, kept within the east forest edge until they moved south.

The indigo bunting *(Passerina cyanea)* showed tendencies toward territorial selection which were limited to the defense of the areas around the singing posts during the mating and breeding period in early June. After the nests were built and the eggs laid, the males continued to retain their original singing posts, which, in all cases, were within three to five meters of the nest. After the young hatched, it became apparent that the whole nesting population used a large feeding range, the limits of which took in all of the nests (Fig. 6, No. A). The buntings, which formed a social group, were unlike the other forest nesting species in their territorial behavior, at least insofar as feeding was concerned. Howard (1920) says that buntings [*Emberiza schoeniclus*] desert their territories temporarily and collect in flocks on the newly sown fields of grain. He observed that they established a territory in the early part of the season, but when food became scarce, they were forced to range out to places where there was an abundance of food.

HIGH SHRUB SOCIETY

This society supported only two species of nesting birds, the red-eyed vireo and the wood pewee, but many of the birds from other societies expanded their territories slightly into this community. The cardinal, indigo bunting and tufted titmouse established secondary singing posts and, along with the downy woodpecker and wood thrush, gleaned insect food from this layer.

The selection of territories by the red-eyed vireo *(Vireo olivaceus)* was a rather passive affair, carried out by the male. When the migration reached its maximum early in May, there was a great deal of chasing between males and females, often with three or four birds taking part. Finally, when only the breeding population remained, the birds mated. It was easy to locate the individual nesting pairs by the singing males (Fig. 7, No. B). Each male retained a singing post in the upper canopy throughout the summer. The vireos were decidedly solitary in their nesting habits. No two pairs nested close to each other but were well spaced over the forest. They occupied the middle layer or high shrub society which extended from three meters above the ground to just below the canopy (about 12 meters), thus giving them a wide choice of nesting sites. The outer limits of the territories were not clearly ascertained until after the young had hatched. Most of the food was obtained from the vegetation relatively close to the nest. The young left the nests by the first of
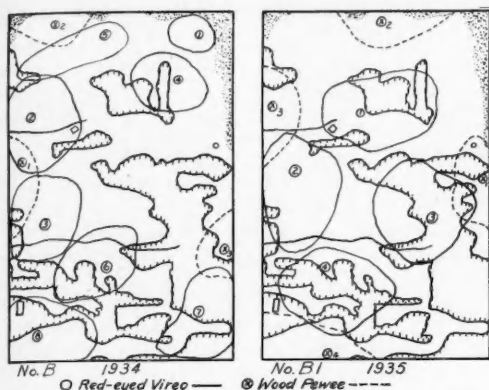
FIG. 7.   Nests and territories.   High shrub society.
B, 1934; B₁, 1935.   See Fig. 6.

No.B   1934   No.B1   1935
O Red-eyed Vireo——   ⊗ Wood Pewee-----

July and became very seclusive in the dense foliage. By the serotinal period they dispersed, leaving only the adults.

Almost as soon as the migrants left, the wood pewee *(Myiochanes virens)* chose its territory. This flycatcher was easily located because of its activity and continual singing as it fed along the edge of the forest. Territories, which were never large and always extended to the forest edge, were established even before the nests were built (Fig. 7, No. B1; Table 2). The birds seldom traveled more than 100 yards from the vicinity of the nests. One or the

other of the adults habitually alighted on some dead branch overhanging the forest edge, or on a fence, and from such perches flew out and caught passing insects. When the young hatched at the end of the first week of July, vigorous feeding activities did not alter the territories. The adults continued to occupy the same perches or remained within a few meters of them. After young left the nests, family groups moved along the edge of the forest without any indication of territory. Family groups gradually broke up between the first of August and their departure in September. It was common to see individual birds catching flying insects and showing no apparent interest in others of their own species. This behavior is characteristic of most flycatchers with the approach of the migration period.

TREE TRUNK SOCIETY

This community is not a true layer society for it includes an area from the base of the trees to the upper branches. Because of their structural specialization, the downy woodpecker, red-headed woodpecker and white-breasted nuthatch comprise this distinct community. The only competitors are such birds as the tufted titmouse, starling and crested flycatcher. These birds use old woodpecker holes for nests and establish territories which reach into one or more of the recognized layer societies.

By the first week of May the downy woodpecker *(Dryobates pubescens medianus)* became a forest dweller. During a brief interval between April 28 and May, the downies were heard throughout the

TABLE 2.   Territory size within the layer societies.

Ground-Low Shrub Society	1934			1935		
	Average size of individual territories in hectares	Available area in hectares per pair	Number of pairs	Average size of individual territories in hectares	Available area in hectares per pair	Number of pairs
Indigo Bunting	.23	1.1	22	.24	1.1	21
Wood Thrush	2.7	7.0	3	2.7	7.0	3
Cardinal	3.3	7.0	3	3.3	7.0	3
Maryland Yellow-throat	1.5	11.0	2	3.0	22.0	1
High Shrub Society						
Red-eyed Vireo	2.3	3.0	8	4.5	6.0	4
Wood Pewee	3.3	8.0	3	2.5	2.4	4
Canopy Society						
Crested Flycatcher	4.4	4.8	5	5.5	6.0	4
Yellow-billed Cuckoo	11.0	11.0	2	22.0	22.0	1
Tree Trunk Society						
Downy Woodpecker	4.4	4.8	5	5.5	6.0	4
Red-headed Woodpecker	5.5	6.0	4	11.0	11.0	2
White-breasted Nuthatch	22.0	22.0	1	....	....	
Barred Owl	22.0	22.0	1	22.0	22.0	1
Tufted Titmouse	4.8	4.8	5	6.0	6.0	4

Total pairs.. 73 62
Hectares per pair of total population.............. .30 .... .32
Acres per pair of total population.................. .74 .... .79

daylight hours, but there was no evidence that territories had been established. Two males were often seen pursuing a single female. The birds were found mated on May 10, and each pair had its separate territory. Nesting holes were constructed in dead portions of large limbs or tree trunks. Pairs were distributed evenly over the forest with individual nests widely separated. In 1934 there were five nests, while in 1935 there were only four. There was no overlapping of nesting territories. They were comparatively uniform in size and did not comprise the full extent of the forest area, although in 1935 they were slightly larger than in 1934 (Fig. 8, No. C;

No. C   1934   -   No. C1   1935
⊗, Downy Woodpecker——   O Red-headed Woodpecker----
O White-breasted Nuthatch——·—— · ⊗ Starling ● Barred Owl

FIG. 8. Birds nests and territories. Tree trunk society.

Table 2). With the hatching of the young in early June, the adults became more active but seldom flew more than 50 meters from the nest in 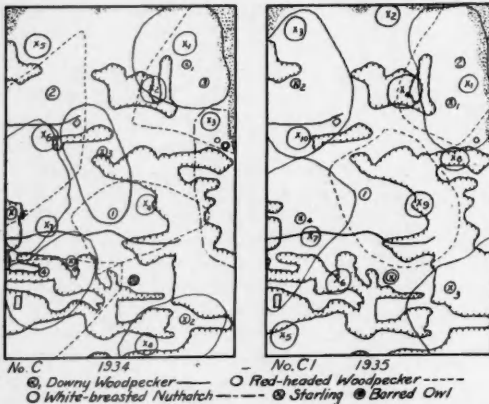search of food. On an average, the young were fed every 3.05 minutes by one or the other of the parents. The male left the nest in one direction; the female in the opposite, and the directions shifted from day to day. Territories were abandoned as soon as the young left the nest. The adults took the young into the dense foliage of the canopy and left them while they went in search of food. The young were able to take care of themselves by the late aestival period, after which time they left the woods. The adults remained and moved to the forest edge. There was never any indication of winter ranges. Singly or in small groups of three or four, the birds traveled over the forest and forest edge according to changing weather conditions.

In at least one instance the red-headed woodpecker (*Melanerpes erythrocephalus*) showed pronounced territoral inclinations. In 1934 a pair of woodpeckers (Fig. 8, No. C1, nest 2) selected a tall, dead sycamore in the center of the woods, which, from the number of old holes present, had been a favorite nesting site. A pair of crested flycatchers had built their nest in one of these holes, and the female was sitting on her five eggs. On June 23, 1934, while censusing the woods, the writer heard a great commotion in

the direction of the crested flycatchers' nest. Two red-headed woodpeckers, a male and a female, were busy fighting off the flycatchers and at the same time going into the flycatchers' nest, throwing out the feathers and, finally, the eggs. By the end of an hour the flycatchers were ejected from their nest. The following day the red-heads, rather than take the hole which the flycatchers had used, proceeded to build a new one directly below the flycatcher nest. They completed the nesting hole on the third day, June 27, and a brood of four red-headed woodpeckers left the nest on July 28. In 1934 four pairs nested in the woods. In 1935 the two nesting pairs occupied the same nesting sites as did numbers 1 and 3 in 1934, but the 1935 territories were larger. By the time the young were able to come to the entrance of the nesting holes, the parents had extended their territories to the limits indicated in Fig. 8, No. C1; Table 2. These territories were retained for a short time after the young left the nest. They were broken by the first of August, and the families moved to the forest edge. The adults continued to feed the young until the middle of August, even though they were fully grown. While the young rested on a fence post, the adults caught flies, grasshoppers, and hymenopterous insects. The wintering birds wandered throughout the forest, singly or in pairs.

A pair of the white-breasted nuthatches (*Sitta carolinensis carolinensis*) spent the winter in the elm-maple forest during 1934. Their winter feeding range comprised the entire woods. Throughout the hiemal period the birds spent over half their time in the locality which was to be their nesting site. This conforms with the studies of Butts (1931) who found that all nests of the white-breasted nuthatch were within five hundred yards of the place where the birds had been captured during the winter. The nests were built within or near these ranges, and, in general, the nesting territories and winter ranges coincided fairly well. In the elm-maple forest, the birds began to show a more active interest in each other and frequently appeared together as the prevernal period approached. Their wanderings throughout the forest became less noticeable toward the end of this aspect. At the beginning of the vernal period two additional males arrived, and intense activity was exhibited during the following few days as mating began. Eventually, the two extra males left, and the pair of resident nuthatches chose a nesting site in a large elm. Between May 20 and 25 both birds participated in the nest building, chipping out wood on the under side of a dead limb. The male stayed close to the nest until the young hatched on June 10. In the subsequent feeding activities there were suggestions of a restricted territory (Fig. 8, No. C; Table 2). The adults did not travel far for food; they seemed to procure it in sufficient quantities from the surrounding trees. Butts (1931) reported that although the birds which he observed traveled considerable distances from the nests, they also obtained an abundance of food close to the actual nesting sites. In the present study the young were found to leave

the nest on June 30, and the family group, consisting of four young and the two parents, remained in the vicinity of the nesting territory until the middle of July. Throughout this time the adults carefully watched and fed the young. Then the young disappeared, and the adults established their hiemal range. Butts (1931) mentioned that he did not succeed in banding any young but noticed that a number of young appeared at a neighboring station a half mile away, where they remained all winter. Whittle (1926) found that the young left the parents or, perhaps, were driven away, in July.

Figure 9, No. C2 represents the territories established by nine pair of tufted titmice *(Baeolophus bicolor)*—five in 1934 and four in 1935. These territories were discovered early in the mating season, during the last of April and the first week of May.

No. C2 1934, 1935
⊗ Tufted Titmouse 1934
⦶ Tufted Titmouse 1935

No. D 1934, 1935
⊗ Crested Flycatcher 1934—, X 1935—
⊗ Ruby-throated Hummingbird 1934, ⦶ 1935
⦶ Yellow-billed Cuckoo 1935-----
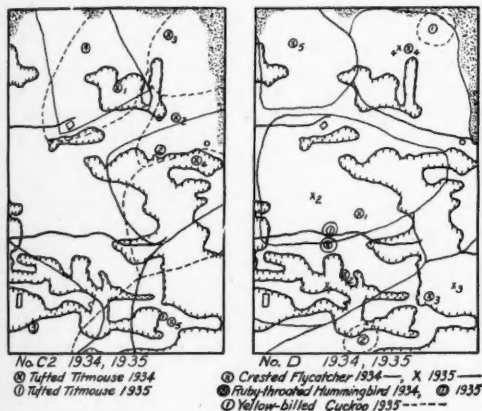
FIG. 9. Birds nests and territories. Tree trunk society. C, 1934; C₁, 1935. See Fig. 6.

The singing birds were invariably heard from the same localities, and the mated pairs were seen at the same places each day. The nests were located by observing the movements of both birds when together, or when one was carrying nesting material. When the young hatched out, the actual limits of the territories were ascertained by watching the movements of the adults as they left the nests for food. The distances traveled were plotted on a map, and by the time the young were able to leave the nests, the limits of these territories were well defined (Fig. 9, No. C2; Table 2). No two territories overlapped. They were well spaced over the forest, and the birds always stayed within their territorial limits. There was no apparent competition with other breeding species, for the time of nesting was several weeks earlier. On an average, the nests were located 15 or more feet above the ground, and the feeding activities were confined to the higher shrubs and upper tree canopy. By August there was a dispersal of some family groups out of the forest while the remaining birds roamed over the whole forest. During the two years studied, the titmouse population tended to remain fairly uniform, although it was not so large from late serotinal

to the prevernal aspect as during the rest of the year. During the hiemal period there was no evidence of a limited winter range. The birds wandered over the whole forest in bands of four or five (probably family groups). Their movements were governed by changes in weather conditions. With a rise in temperature, they moved into the forest, and with a drop, they shifted to the east forest edge. During the winters of a four-year period, Gillespie (1930) found that tufted titmice traveled in small bands, suggesting family groups, and occupied definite and limited areas which never overlapped.

The starling *(Sturnus vulgaris vulgaris)* wandered freely over the forest proper, but had a limited territory around the immediate nesting site. The essential nesting requirement was an old woodpecker hole or a natural cavity. Two pairs of starlings never nested in the same dead tree, no matter how many holes were in it, and thus indicated their preference for isolation at this time. Other birds were tolerated close to the nesting tree but were not permitted to alight on it. Upon one occasion an eastern bluebird's partially finished nest was destroyed by a pair of starlings which later occupied the same hole and successfully raised their own family. Eight nests were located in 1934 and ten in 1935 (Fig. 8, No. C1). As the young hatched, the starlings became more aggressive and attempted to drive off any intruders—bird or mammal. They all had young by May 20 and moved out to the forest edge and open fields where they scratched over the ground in search of beetle larvae, spiders, earthworms, lepidopterous larvae and other soft-bodied insect types. While the nesting territory was distinct, the feeding range was not well defined and covered a wide area. The starlings might then be considered merely as visitors in the forest for about five or six weeks during which time they received shelter for the raising of their young.

The barred owl *(Strix varia varia)* spent most of its time in the woods, and, since there were few other large birds of prey, the owl took in the whole forest and its edge as a feeding range and as territory during the breeding season. The pair was seldom seen together except during the mating season. At all other times they were within calling distance, but displayed only a passive interest in each other. This indicates that they probably were mated for the year and that they renewed their activity just before the nesting period.

UPPER CANOPY SOCIETY

This community is used by numerous birds for gathering food, protection from enemies, shelter, and also, by a few, for the establishment of nesting territories. The yellow-billed cuckoo, ruby-throated hummingbird, and crested flycatcher made up the nesting population.

The yellow-billed cuckoo *(Coccyzus americanus americanus)* was one of the last birds to arrive. Cuckoos appeared in early June and remained almost exclusively in the upper canopy. There, in the dense crown of the forest, they hunted insect larvae, running along the branches but seldom flying more than

a few yards. The male of each pair began calling from specific localities in the upper canopy before the nest was built. The three nests observed were all over ten feet from the ground in the high shrubs. The territories defended by the males were principally from the immediate nesting site to the limits of the individual singing posts in the upper canopy. Since the greater part of their activity was confined to the upper canopy, they are here treated as belonging to this society. The male cuckoo became much disturbed at the close approach of any other bird and drove the intruder from the vicinity of the nest. On the other hand, the feeding range could not be included as a part of the territory for it covered the whole forest canopy and was not defended.

A pair of ruby-throated hummingbirds *(Archilochus colubris)* arrived about the first of July and immediately constructed a nest. In 1934 the nest was 25 feet up in a pawpaw in the center of the woods; in 1935 a pair nested 40 feet up in a large maple tree, out on the farthest tip of a branch (Fig. 9, No. D). The birds avoided the west and northwest forest edges for the east, northeast, and south edges which were abundant with trumpet weed and numerous other flowering plants. For the most part, the birds stayed in the tops of the higher shrubs and forest canopy from whence they darted down to the dense foliage of the forest edge. The hummingbirds had well-established territories, especially in relation to nests. No other bird, regardless of its size, was permitted to approach within ten meters. Even the female was belligerent and did not allow another bird to fly by when there were young in the nest. It was not uncommon to see her chasing off a red-headed woodpecker or even a crow. The chief mode of attack was to fly at the intruder and buzz about the back of its head, a procedure which was most annoying to the trespasser. The female did the incubating, feeding, and caring for the young. The feeding range, which covered the greater part of the woods, was not so well defined as the territory.

The crested flycatcher *(Myiarchus crinitus boreus)* arrived singly or in pairs in early May and wandered over the forest and its edge in search of insects in the higher shrubs and canopy. On only a few occasions were birds seen catching flying insects in the low shrubs. Soon mating calls came consistently from definite localities, and by the first week of June, territories were established. The nests occupied were in the old holes of the red-headed woodpecker or flicker, 40 to 50 feet from the ground. The only competition over nesting holes was with the red-headed woodpecker. A pair of these birds chose to nest in the same tree already tenanted by a pair of flycatchers. As mentioned earlier, the battle terminated in the woodpeckers throwing the nest and eggs out of the hole and then constructing a new nest below that of the flycatchers'.

Five territories were established in 1934 and four in 1935 (Fig. 9, No. D). They were comparatively large, each covering about one-fifth to one-fourth of

the forest canopy (Table 2). Nests 1, 2, and 3 in 1935 were close to the actual nesting sites of 1, 2, and 3 of 1934, and the birds occupied approximately the same territories. Nest 4 in 1934 was again used in 1935. The young hatched by the middle of June in both years and left their nesting holes in early July. The territories were broken as the birds scattered throughout the forest.

The cowbird *(Molothrus ater ater)* showed no signs of territorial selection. The birds ranged in small groups, generally three or four females and one or two males, throughout the forest and forest edge. The females spent much of their time locating other birds' nests in which to deposit their eggs. The selection of females was accompanied by some combat among the male birds, but there was no evidence shown that cowbirds select and protect a territory. Friedmann (1929) found that *Molothrus ater ater* does not have a territory. Likewise, Nice (1933 b), in speaking of the cowbird, points out: "I have banded a number of breeding adults of this species near our home; in 1931 one female was seen on her summer range as late as September 13, and the next year even until October 3. These birds are entirely friendly to one another throughout the summer; two females, one banded and the other not, regularly roamed about together in a 30-acre tract, and two others, again one banded and the other not, did likewise on another 30-acre tract further north. A banded male consorted with all these females and with still another banded female still further to the north; there were also a number of unbanded males that lived in the same region. Of course, cowbirds do not feed young, nor do they repell [sic] rivals to ensure their offspring less competition. *Molothrus ater* cannot be said to have a 'territory,' when it never defends it."

SEASONAL SOCIETIES

Toward the end of the serotinal period and the beginning of the autumnal migration, the layer societies were no longer apparent (Fig. 3). With the development of the young birds, there was a dispersal of the general breeding populations, followed somewhat closely by the arrival of the first migrants. At this time the birds wandered throughout the forest. The autumnal migration peak was greatest on the forest edge, where it coincided with the newly concentrated masses of agricultural and prairie insects.

The east half of the forest, and especially the east and south forest edges, constituted the major area covered by the winter ranges of the hiemal and perennial birds. There were no particular territorial boundaries between species or individuals other than the structural limitations of the birds in the community. The ground cover of the forest edge was the most pronounced layer. The heavy mat of dead leaves and the dense undergrowth of shrubs and herbs afforded an excellent place of shelter and food for tree sparrows, juncos, cardinals, Carolina wrens, tufted titmice, robins and song sparrows. Usually in flocks of five to fifty, the birds fed extensively on seeds, berries, and insects scratched from the ground

cover of leaves. Actually, then, groups of birds rather than individuals chose the feeding ranges which were very flexible, shifting with changes in the weather and available food supply. Since no combat was involved, there was no evidence of a defended territory.

The robin was an influent in the ground society from the middle of January to the end of March. Both in 1934 and 1935, a flock of about 40 robins appeared in the south third of the forest by January 20. They spent the greater part of their time on the ground, scratching among the dead leaves. By the end of February, the whole south third of the forest looked as if a flock of chickens had been scratching over the forest floor. Throughout the stay of the robins, 12 stomach contents were examined at intervals and found to contain large numbers of white Bibio larvae. One stomach contained 40 larvae, another 35—representing 92 per cent of their entire food. In addition to these larvae, the stomachs contained Coleoptera, Carabidae, Hemiptera, Arachnida and small amounts of vegetable food. Assuming that the 40 robins each consumed 40 Bibio larvae per day, approximately 96,000 of these larvae were accounted for in the two months. Bibio larvae disappeared in the forest by the end of March and none was found in the numerous soil samples examined. Forbes (1880) described a similar incident during February and March at Normal, Illinois. In one stomach, he found 175 Bibio larvae, which further brings out the preference of robins for this type of insect.

The food of the tufted titmice was diversified. Their activities on the ground and shrub layers were somewhat indefinite so that they did not interfere to any extent with other birds. Since their numbers were comparatively large (10 to 14 individuals), and because of their permanency in the forest, they should be regarded as minor influents.

The tree sparrows and juncos occupied a somewhat separate niche on the east and south forest edge which afforded them shelter and an ample supply of weed and grass seeds. These minor influents, in flocks of 50 to 100, were found consistently throughout the hiemal period. The effect of the one pair of Carolina wrens was negligible.

The principal occupants of the tree trunk society were the downy, hairy, red-headed and red-bellied woodpeckers, the white-breasted nuthatch, brown creeper and tufted titmouse. These birds did not indicate very specific ranges within the forest and showed changes with wind exposure. Frequent west and northwest winds drove them to the east forest edge. Food was not a factor, for on calm days, when the atmospheric temperature was fairly uniform, the birds of this society scattered over the whole woods—the nuthatches, creepers and titmice looking over the surface of the bark, and the woodpeckers chipping out rotten and dead stumps in search of beetle larvae.

During both the northward and southward migrations, there was no particular stratification. In the spring, the migrant birds moved through the forest and along its edges in waves that increased in magnitude as the peak was reached and then gradually decreased to a minimum as the breeding birds became stable with the selection of territories in one or more of the recognized layers.

NESTING STATISTICS

A study to determine the percentage survival of the young was made of three species; the indigo bunting, red-eyed vireo, and wood thrush. The final percentage values are only relative for in order to establish a survival rate, it would be necessary to evaluate critically a much larger area over a period of years.

The most destructive enemy of the indigo bunting is the cowbird. Its parasitic habit of laying eggs in other bird's nests is well known, but the effect which this has upon the increase of other birds is not so well understood. Tables 3 and 4 disclose that 112 bunting eggs and 22 cowbird eggs were laid in the 41 buntings' nests built in 1934 and 1935. The growth curves (Fig. 11) indicate that, at the time of hatching, the cowbird has a distinct advantage in size and weight over the bunting. The growth of the cowbird is very rapid, for it is able to monopolize most of the food, and in consequence, the other young birds are either pushed out of the nest or trampled to death. Figure 11a shows the normal development of three buntings. In a nest occupied by three buntings and one cowbird (Fig. 11b) one bunting was pushed out the second day after hatching; the other two were able to withstand the competition until they left the nest. In another nest three buntings and two cowbirds hatched (Fig. 11c). One bunting was pushed out by the end of the first five days; another was ejected on the eighth day and the third on the eleventh day. The two cowbirds thrived normally and on the thirteenth day crowded themselves out of the nest, but they had advanced enough to hop about among the shrubs.

The effect of the cowbird is significant. In 1934 (Table 3) 57.0% of the buntings and 53.8% of the cowbirds successfully left the nests. In 1935 it was 59.0% of the buntings compared to 100% of the cowbirds (Table 4). In 1934, 23.8% of the buntings were destroyed by the cowbirds as against 31.7% in 1935.

Other enemies of buntings were few indeed. Cats destroyed 22% of the bunting young in 1934 and were responsible for 8.8% of the mortality in 1935. No estimates could be made of the numbers of birds killed after leaving the nests. In 1934, 12.3% of the eggs were destroyed by snakes (*Lampropeltis* sp.), but in 1935 none was molested in this way. Twenty-two per cent of the nests were abandoned in 1934 and 36.8% in 1935. The cause of these desertions was undetermined. The nests were completed, but no eggs laid. Whether the adults met with misfortune or merely built additional nests was never established.

Figure 11 (a, b, c) shows the rate of growth of young indigo buntings and cowbirds during the first ten to twelve days after hatching. The growth curves are steep, showing an average daily growth of about

TABLE 3. Nesting statistics of the indigo bunting, 1934.

Nest Number	Number of Bunting eggs	Number of Buntings hatched	Number of Cowbird eggs	Number of Cowbirds hatched	Young Buntings destroyed by Cowbird young	Eggs taken by snakes	Young taken by cats	Nests deserted	Buntings that successfully left nest	Cowbirds that successfully left nest
1....	4	0	..	..	..	4	..	..	..	..
2....	4	3	..	..	..	..	3	..	..	..
3....	2	0	..	..	..	..	..	..	..	..
4....	3	3	1	1	1	..	..	..	2	1
5....	3	3	..	..	..	..	..	..	3	..
6....	..	..	..	..	..	..	..	1	..	..
7....	3	3	..	..	..	..	..	..	3	..
8....	4	4	2	0	..	..	..	..	4	..
9....	3	3	..	..	..	..	..	..	2	..
10....	..	..	..	..	..	..	..	1	..	..
11....	..	..	..	..	..	..	..	1	..	..
12....	3	3	..	..	..	..	..	..	3	..
13....	4	0	1	0	..	5	..	..	..	..
14....	3	0	1	0	..	..	..	1	..	..
15....	3	3	2	2	3	..	..	..	..	2
16....	..	..	..	..	..	..	..	1	..	..
17....	3	3	1	1	2	..	..	..	1	1
18....	4	3	1	0	..	..	..	..	3	..
19....	4	4	..	..	..	..	4	..	..	..
20....	4	4	1	1	3	..	..	..	1	1
21....	4	4	1	1	1	..	4	..	..	..
22....	2	2	2	2	..	..	..	..	2	2
Total.	60	42	13	8	10	9	11	5	24	7
Per cent.	..	70%	..	61.5%	23.8%	12.3%	22%	22.7%	57%	53.8%

TABLE 4. Nesting statistics of the indigo bunting, 1935.

Nest Number	Number of Bunting eggs	Number of Buntings hatched	Number of Cowbird eggs	Number of Cowbirds hatched	Young Buntings destroyed by Cowbird young	Young taken by cats	Nests deserted	Buntings that successfully left nest	Cowbirds that successfully left nest
1.....	..	..	..	..	..	..	1	..	..
2.....	..	..	..	..	..	..	1	..	..
3.....	4	4	1	1	2	..	..	2	1
4.....	4	0	..	..	..	..	1	..	..
5.....	5	5	..	..	..	..	..	5	..
6.....	4	4	..	..	..	..	..	4	..
7.....	1	0	..	..	..	..	1	..	..
8.....	4	4	..	..	..	..	..	4	..
9.....	4	4	1	1	3	..	..	1	1
10.....	3	2	2	2	2	..	..	0	2
11.....	2	0	..	..	..	..	1	..	..
12.....	3	3	2	1	1	..	..	2	1
13.....	3	3	1	1	2	..	..	1	1
14.....	4	4	..	..	..	4	..	..	..
15.....	3	3	2	2	3	..	..	0	2
16.....	..	..	..	..	..	..	1	..	..
17.....	4	4	..	..	..	..	..	3	..
18.....	..	..	..	..	..	..	1	..	..
19.....	4	4	..	..	..	..	..	4	..
Total...	52	44	9	8	13	4	7	26	8
Per cent..	..	84.6%	..	88.8%	31.7%	8.8%	36.8%	59.0%	100%
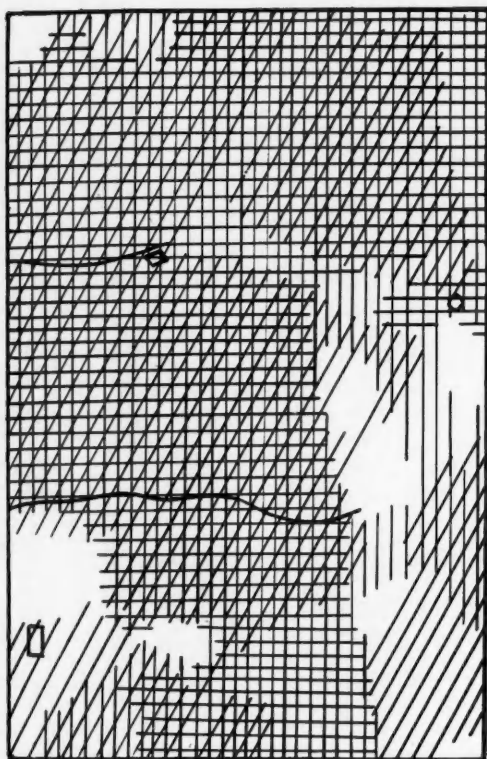
FIG. 10. Vegetation and territory maps. A composite of all nesting territories in the elm-maple forest. Horizontal lines indicate the area covered by territories of birds nesting on the ground and in low shrubs. Oblique lines indicate the area covered by territories of birds nesting in tree trunks. Vertical lines indicate the area covered by territories of birds nesting in high shrubs and the forest canopy. Compare with Figs. 1, 6 to 9. Note avoidance of the climax.

one gram which, in the first day or two, represents an increase of one-half their body weight. Great numbers of insects must be consumed each day to effect this gain. The amount of food eaten by a family of four young buntings during a 12-hour day between 6 A.M. and 6 P.M. was estimated. One or the other of the parent birds brought an average of five insects to the nest every 15 minutes, making a total of 60 insects for each young bird per day, or 960 insects from the time of hatching until leaving the nest. For the 26 buntings that successfully left their nests in 1934 and the 25 in 1935, the consumption for each year totaled roughly 25,000 insects taken from 2.53 hectares (6.25 acres) during the time spent in the nests.

In 1934, three nests of the wood thrush, containing four eggs each, were located (Table 5). A cowbird's egg was found in nest 1 the first day after the thrush had finished laying, but the whole complement of

eggs was destroyed by bronzed grackles after the tenth day of incubation. Nest 2 contained four thrush eggs and one cowbird egg. One thrush egg and the cowbird egg failed to hatch. The three young thrushes were successfully raised. All of the eggs in nest 3 hatched and left the nest. During this season 58.3% of the young left the nest successfully, while 33.3% were destroyed by bronzed grackles. Since only three nests are represented, the percentage values should be regarded only as relative values.

Again in 1935 only three pairs of wood thrushes nested in the forest (Table 5). Nests 1 and 3 contained four eggs each, which were successfully hatched and raised. Nest 2 contained three thrush eggs and one cowbird egg. All were hatched and raised. Since the nest was not overcrowded, and the cowbird young was nearly the same size as the thrush young at hatching, all developed at the same rate and left the nest together on the 13th day. The low mortality may be attributed to the larger size of the nest, the fact that it is less exposed than the nests of the forest-edge birds, and to the more seclusive habits of the thrushes.

Eight red-eyed vireo nests were studied in 1934 and four in 1935. The nests were from one to five meters from the ground and always in the dense foliage of pawpaw or young basswood. Nidification began during the first week of June, and by the middle of the month, all of the nests contained eggs. In 1934, there
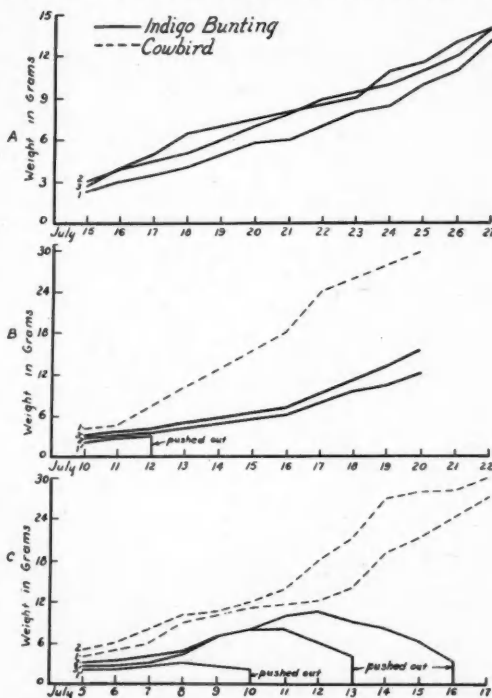
FIG. 11. Growth curves of nestlings. a. Three indigo buntings in normal development. b. The effect of one cowbird in a nest of three indigo buntings. c. The effect of two cowbirds in a nest of three indigo buntings.

were 24 eggs laid in the eight nests with an average of three per nest. Almost as soon as the vireos started to lay, cowbirds deposited eight eggs in six of the nests (Table 6). The eggs began hatching by June 28 in both years. Immediately after the hatch-

TABLE 5. Nesting statistics of the wood thrush, 1934 and 1935.

|				1934			
Nest	Number eggs	Eggs hatched	Number Cowbird eggs	Eggs destroyed by grackles	Cowbirds hatched	Thrushes success-fully left nest	Cowbirds success-fully left nest
1......	4	0	1	4	0	0	0
2......	4	3	1	0	0	3	0
3......	4	4	0	0	0	4	0
Total ..	12	7	2	4	0	7	0
		58.3%		33.3%		100%	

			1935			
Nest	Number eggs	Eggs hatched	Number Cowbird eggs	Cowbirds hatched	Successful Thrushes	Successful Cowbirds
1.......	4	4	0	0	4	0
2.......	3	3	1	1	3	1
3.......	4	4	0	0	4	0
Total...	11	11	1	1	11	1
		100%		100%	100%	100%

ing of the last bird, both adults fed the young, displaying no discrimination between their own progeny and those of the cowbirds. Throughout the entire feeding of the young, an insect diet consisting of large numbers of Arachnida, larval and adult Lepidoptera, assassin-bugs, tree hoppers, and chinch-bugs was administered. Stomach analyses revealed that the adults consumed the same kind of food that they fed their young. Herrick (1901) reported that a female was observed feeding raspberries and blackberries to the young on the third day after hatching. The vireos studied by the author were never noticed feeding the young any form of vegetable food.

Of the 24 vireo eggs, 66 per cent hatched, and of these, 81 per cent of the young birds left the nest (Table 6). On the other hand, 75 per cent of the cowbird eggs hatched, and of these, 100 per cent left the nest. Eighteen per cent of the vireos that hatched were pushed out of the nest by young cowbirds. One vireo nest was deserted.

In 1935 there was a drop in the nesting population; only four pairs of vireos built nests and raised young. Of the 15 eggs laid, 86.6 per cent hatched, but only 53.8 per cent of these left the nest. Cowbirds parasitized all four nests with 100 per cent hatching and 80 per cent of the young leaving the nest. A total of 46 per cent of the red-eyed vireos were directly destroyed through eviction from their nests by the larger cowbird young.

Predation by the cowbird, and to a limited degree,

TABLE 6. Nesting statistics of the red-eyed vireo, 1934.

					1934			
Nest Number	Vireo eggs laid	Vireo eggs hatched	Cowbird eggs laid	Cowbird eggs hatched	Vireo nests deserted	Young Vireos destroyed by Cowbirds	Vireos that were successfully raised	Cowbirds that were successfully raised
1..........	2	1	2	2	..	..	1	2
2..........	4	3	1	1	..	1	2	1
3..........	3	3	1	0	..	..	3	0
4..........	1	1	2	1	..	1	0	1
5..........	4	0	..	..	1	..	..	..
6..........	2	2	1	1	..	..	2	1
7..........	3	2	1	1	..	1	1	1
8..........	5	4	..	..	..	..	4	..
Total......	24	16	8	6	1	3	13	6
Percent....	..	66%	..	75%	12.5%	18%	81%	100%

				1935			
Nest Number	Vireo eggs laid	Vireo eggs hatched	Cowbird eggs laid	Cowbird eggs hatched	Young Vireos destroyed by Cowbirds	Vireos that were success-fully raised	Cowbirds that were success-fully raised
1........	4	4	1	1	2	2	1
2........	5	4	1	1	1	3	1
3........	3	2	2	2	2	0	1
4........	3	3	1	1	1	2	1
Total.....	15	13	5	5	6	7	4
Percent...	..	86.6%	..	100%	46%	53.8%	80%

by the domestic house cat and bronzed grackle, was considered to be the primary cause adversely affecting the ultimate success of the passerine fledglings under discussion. Kendeigh (1942) made an analysis of a large number of nesting birds. He regarded a nesting attempt to be successful when at least one bird was raised to the point of leaving the nest, regardless of the other young or eggs. Throughout the territorial studies reported in the present paper, the number of nests for each species observed was relatively small so that only percentage values of species chosen for nesting statistics can be compared with those noted by Kendeigh (Table 7).

TABLE 7. Comparison of nesting success 1934-1935 with 1942.

Species	Elm-Maple Forest		Kendeigh (1942)	
	Number Nests	Percent Success	Number Nests	Percent Success
Red-eyed Vireo......	12	75	13	62
Wood Thrush........	6	83	16	73
Indigo Bunting.......	41	43.9	..	..
Bluebird............	..	..	142	60
Starling.............	..	..	21	76
Cardinal............	..	..	11	82
Crested Flycatcher...	..	..	7	43

These "successes" are naturally subject to variable environmental factors so that any such set of figures must be very critically examined before any semblance of a conclusion can be drawn. An undisturbed community would undoubtedly afford an ample food supply, more cover, and predation would be at a relatively uniform level. Nice (1937) states that in normal years when there is adequate cover and food, the song sparrow population had a high percentage survival rate for nestlings, and predation was at a minimum. In adverse years when survival rate was very low, the decrease was directly accountable to the disturbance of the nesting territory by man, or in some years, by drought or flooding. The unfavorable years were always accompanied by a decrease in available shelter and food supply and an increase in predation. In his study of 1,056 nests of the house wren, Kendeigh (1942) found that the average percentage of eggs which failed to hatch is constant within the temperature range of 58°-70° F. A drop or rise of temperature beyond this range brought about a rise in the percentage of eggs that did not hatch. These observations strongly emphasize the critical effect of temperature and to some extent, humidity, upon the optimum of environmental factors necessary for the survival of a species (Twomey, 1936).

POPULATION DENSITY AND CARRYING CAPACITY

The most suitable method that I know for determining the population density of the woods during the breeding season is to count nesting species and note their territories. Williams (1936) also found this procedure satisfactory. Table 2 shows the nesting population density of the elm-maple forest. During the years 1934 and 1935, there was little difference in the total number of nesting pairs; in 1934 there were 0.3 hectares per pair, and in 1935, 0.32 hectares per pair. The territories were stratified into layer societies but did not cover the total area of each community. In each society there were species limitations (structural adaptations) as well as such environmental limitations as wind velocity, temperature, exposure of nesting sites, cover, food supply, predation, etc., with respect to the amount of available territory.

The distribution of the nesting population indicates an individual species selection of suitable territories. The comparative stability of the total population for each layer society gives some idea of the possible carrying capacity of the elm-maple forest during the nesting period. Errington & Hamerstrom (1936) refer to the winter carrying capacity of the northern bob-white (*Colinus virginianus virginianus*) ". . . as denoting the upper limit of survival possible in a given territory as it exists under the most favorable conditions." Carrying capacity, as applied to the elm-maple forest, designates the number of pairs per hectare of the total nesting population and is comparatively uniform from year to year. There is a normal survival and reproductive rate and no apparent overcrowding of available nesting territories or food ranges.

There are many factors that limit the carrying capacity of any given community. Wind velocity, temperature, exposure of nesting sites, cover, food supply, etc., affect the availability of suitable nesting sites within a community. Over 75% of the nesting territories were in the east two-thirds of the woods. The prevailing winds from the southwest may have been partly responsible for the decrease in nests in the west one-third of the forest. Kendeigh and Baldwin (1937) give the following factors that affect yearly abundance: "first, the number of adults at the beginning of the breeding season; second, the amount of reproduction, measured by the percentage increase in total number of individuals due to the raising of young during the breeding season; and third, the loss in number or mortality of adults and young from the breeding season of one year to the beginning of the breeding season of the next year."

Predation is also an important factor in controlling population densities. The predators in the woods were the barred owl, bronzed grackle, and domestic cat. Parasitism by the cowbird (which may be regarded as a form of predation) was effective in controlling the population increases, and nearly half the population in the forest felt the dint of this agency.

The avian population in the elm-maple forest is subject to great seasonal fluctuations. No two seasons are the same. A study covering a long period of time would, no doubt, bring out more clearly an average population density for each aspect, making it possible to ascertain a carrying capacity for each season of the year in the association.

DISCUSSION OF TERRITORIES

Birds as specialized influents of the elm-maple forest are distinct components of one or more layer societies (Fig. 3). The establishment and stabilization of territories in these layer societies during the mating season is a function of the environment that tends to distribute the population. In a community there is a limit to the area available for nests and territories of any one species of bird. This circumstance, because of cover, food and other factors, automatically sets a maximum population level.

The term "territory" is applied only in the sense of an area that is defended. This, in general, adheres to the concept of the majority of ornithologists who have studied this particular avian reaction. This action is a physiological response or an adjustment which tends to bring the influx of an avian population into the aspects of a biotic community. Previously the behavior of a species was based primarily on its positive reaction to the individuals of its own kind or other species and not as part of the biotic complex.

Defended territories were established about the newly constructed nests and around the singing posts of the males during the breeding season. It was not until the adult birds began feeding young at the nest that the full extent and limitations of each territory became significant in the community.

Territorial space within the community and the resulting apportioning of the food supply during the critical period of a bird's life history (from the beginning of the mating season until the young have left the nest and are able to take care of themselves) should be stressed. In her summary Nice (1933) deduces: "It must be that the food aspect of territory has been overemphasized, and that sex jealously in many cases plays a definite role." Sex jealousy is no doubt apparent in most cases, but may it not be a part of avian activities, the ultimate result of which brings with it stability within the community?

The size in hectares of individual territories is listed and compared with the number of hectares per pair of the total area for the two years (Table 2). It is significant to note that there were more nesting pairs in the woods in 1934 than in 1935. A decrease in the population in 1935 brought an increase in the average size of the individual territories. The stratification of the territories was apparent in the general distribution of the nesting pairs over the forest. There was only a slight overlapping of territories within the layer communities. Nice (1934) emphasized that the song sparrow (*Melospiza melodia beata*) would not allow overcrowding of its nesting territory. She wrote, ". . . each must have approximately two-thirds of an acre for his territory."

In the elm-maple forest there were other factors which affected territorial selection in the community. Figure 10 illustrates a composite of all the nesting territories. Scattered climax areas within the forest were relatively free of nesting territories. The principal nesting population was confined to the late subclimax and forest edge, which afforded more cover

than the climax. Those territories falling within the climax belonged to woodpeckers and nuthatches, species that characterized the tree-trunk society. These same species, however, tended to show a feeding preference for the developmental stages of the community.

Each species showed individual variations in choice of territories and subsequent nesting activities. The indigo bunting had territories only insofar as the actual nesting site was concerned, and the breeding population roamed over a common feeding range. The same was true of the wood thrush although it did not show the social tendencies of the indigo bunting. Starlings had limited territories about the nest and had a feeding range that extended beyond the limits of the forest. Birds that defended a feeding range as a part of their territory exhibited a positive reaction against members of the same species. Other species were tolerated over the feeding part of the territory, but under no circumstance were they allowed to approach the actual nesting site.

The population density for the elm-maple forest in 1934 was 0.3 hectares (0.74 acres) per pair and 0.32 hectares (0.79 acres) per pair in 1935 (Table 2), which shows a relative stability in the avian population with the community during the nesting period.

There were both species and environmental limitations in each society in regard to the amount of available territory. Such limitations were: the structural adaptations of species, wind velocity, temperature, exposure of nesting sites, cover, food supply, etc.

Predation was effective in controlling the yearly population increase as well as being a limiting factor on the nesting population.

REACTIONS AND COACTIONS

The final result of a study of a biotic community is an understanding of the ultimate cause and effect that organisms have upon a habitat and the influence which they exert upon each other. The first is termed a "reaction," while the latter is called a "coaction." The complexity of these interactions in many instances tends to overshadow any individual effect, but through the accumulation of these reactions and coactions, the community emphasizes influences that would otherwise be insignificant.

REACTIONS

Reactions exhibited by terrestrial communities are diminished by the effects exerted upon the soil complex and those that modify aerial factors. Because of the relative protection of the forest from wind, the resulting reaction in the accumulation of falling organic material such as leaves, trees, herbaceous and shrub litter, animal remains, excrement and, to a limited degree, owl pellets, share in the formation of soil.

Reactions by disturbing soil are accumulative in a community. The scratching of the forest floor by robins, starlings, titmice, cardinals, sparrows, and juncos are reactions induced by food coactions. The effect produced by these small passerine birds was

not always noticeable, but, nevertheless, during the late hiemal aspect, large flocks of robins, by their scratching reactions, caused an appreciable turn-over of the forest-floor duff. Likewise, the digging of fox squirrels to store acorns, the innumerable mouse and mole tunnels through the upper foot of the forest floor and the extensive burrowings of earthworms and other invertebrate types all add up to a series of reactions resulting in aeration, decomposition, and ultimate accumulation of forest floor soil.

In discussing air reactions, Clements & Shelford (1939: 91) state: "From the very nature of the medium, the reactions of plants upon the air are usually less definite and controlling than upon the soil. Naturally, the chief reason for this lies in the fact that effects are not readily accumulated in a gaseous medium. However, a notable exception exists in respect to light, in which the time element produces results not unlike those of accumulation. The absence of air reactions by animals is noteworthy since the functions that produce their striking reactions in water are almost without effect on land."

The role of reaction in terrestrial communities is primarily that of the directive function in the succession or competition in the development of the habitat. In the early seral stages, plant reaction brings the establishment of invaders. Succession in a sense is but a series of progressive reactions by which communities succeed each other in such a fashion that only those in closest harmony with the climate will survive. Thus one seral habitat will follow another until the ultimate habitat, the climax, is reached and will become permanent for as long as the climate concerned persists.

FOOD COACTIONS

The food coactions of birds of the elm-maple forest are exemplified in Table 8. On a yearly basis the bird population of the associes was found to be 70%

insectivorous and 30% vegetarian. The seasonal variation of the diet is the most outstanding feature. It explains many of the local movements of the birds within the community (discussed earlier) and also the role played by birds as influent coactors, whether seasonal or perennial, in the community.

The vernal aspect is one of great fluctuation and change throughout the whole community. This trend is shown in the food coactions. The indigo bunting, cardinal, red-headed woodpecker, white-breasted nuthatch, starling, tufted titmouse, and cowbird show a preference for vegetable matter to the extent of 20 to 60% of their total diets; the remainder is composed of miscellaneous insects of which Coleoptera and Diptera predominate. On the other hand, such insectivorous birds as the red-eyed vireo, wood pewee, and crested flycatcher, along with the wood thrush, which is almost wholly insectivorous, feed on a variety of species, but show a choice for the abundant vernal insects; i.e., Coleoptera and Diptera.

The vernal and autumnal aspects are comparable in that they both show great fluctuation in their respective animal populations. Avian migration occurs during both periods and correlates with seasonal rhythms. In the autumnal period the coactions of the insectivorous birds are directed to the selection of the most abundant seasonal types of insects, which include Lepidoptera, Coleoptera, Diptera, and Hymenoptera. The indigo bunting, wood thrush, cardinal, red-headed woodpecker, white-breasted nuthatch, starling, tufted titmouse, and cowbird show a reversal in their food coactions during the autumnal aspect by feeding on the abundant wild fruits and seeds.

The aestival aspect is marked by greater food selection with reference to individual species and to their relative stability within a community. It is

TABLE 8. Food coactions in the elm-maple forest and its margins. The figures are in % of total individuals for insect groups for the season shown. Stomach contents analyses by Lucile A. Rice.

Species	Number of Stomachs	VERNAL						AESTIVAL								AUTUMNAL									HIEMAL					
		Vegetable	Lepidoptera	Coleoptera	Hemiptera	Diptera	Miscellaneous	Lepidoptera	Coleoptera	Hemiptera	Diptera	Hymenoptera	Orthoptera	Homoptera	Miscellaneous	Lepidoptera	Coleoptera	Hemiptera	Diptera	Hymenoptera	Orthoptera	Homoptera	Vegetable	Miscellaneous	Coleoptera	Lepidoptera	Homoptera	Mice and shrew	Vegetable	Miscellaneous
Indigo Bunting	10	15	25	20	...	40	...	50	10	5	20	5	1		9	20	30				40	...	10							
Wood Thrush	6	2	15	16	20	10	37	30	...	10	15	10	...		15	20	15	30	10	5	...		10	...	30					
Maryland Yellow-throat	5	2	...	40	15	10	35	40	30	...	15	...	10	...	5	15	20	5	10	5	20	25								
Cardinal	8	50	...	20	...	...	30	35	20	10	...	...	5	...	30	5	30					60	5		5	...	...	...	90	5
Red-eyed Vireo	6	...	15	25	10	25	25	50	...	...	20	15	...	2	13	20	15	10	20	15	...	15	...	5						
Wood Pewee	4	...	5	10	...	35	50	15	...	...	40	25	10	...	10	10	20	...	50	20										
Downy Woodpecker	8	...	...	70	...	...	30	15	50	...	...	5	...	...	30	...	90				10	...			80	...	8	...	2	10
Red-headed Woodpecker	6	50	...	15	...	...	35	35	20	...	10	10	...	...	25	...	15	...	5	25	10	...	45		20	...	...	...	70	10
White-breasted Nuthatch	7	50	20	10	...	10	10	25	10	...	30	...	...	20	15	...	20	...	15	...	...	20	40	5	2	3	15	...	60	20
Barred Owl	30pl	(85% mice)						(75% mice, 10% birds)								(90% mice and shrew)									(95% mice and shrew)					
Starling	15	50	20	20	...	5	5	20	30	...	15	5	5	...	25	...	2					95	3	(absent)						
Tufted Titmouse	10	20	10	10	5	15	40	25	10	...	18	...	...	...	40	10	20	...	15	5	...	40	10		20	...	...	...	60	20
Crested Flycatcher	5	...	5	20	30	30	15	20	...	10	50	10	...	...	10	15	...	5	40	25	5	...	10							
Yellow-billed Cuckoo	10	...	...	...	...	...	...	80	2	...	10	5	...	...	3	70	5	10	...	5	10									
Ruby-throated Hummingbird	1	...	...	...	...	...	...	...	...	...	20	...	...	...	80															
Cowbird	4	60	10	...	...	...	30	...	...	...	...	...	...	...	...	9						81	10							

pl pellets.

characterized by territorial coactions (competition for suitable mates, nest building, and territorial space within the community for the care and feeding of the young as well as the adults) which illustrate the aestival community relationships of the Aves. This has been fully discussed in relation to territory and layer societies. The young are fed chiefly on the abundant soft-bodied types that contain a high water content such as Lepidoptera and Diptera. Table 8 shows that food selection is prevalent because 15 to 80% of the total food for both young and adults was composed of Lepidoptera and Diptera. It is interesting to note here that, in the analyses, vegetable material was lacking.

The hiemal aspect presents a distinct change in community relationships. All insect life is at a minimum in both activity and numbers. The avian population is likewise reduced to a few species such as the cardinal, red-headed woodpecker, white-breasted nuthatch, and tufted titmouse. These species reverse their food coactions to vegetable diets which are supplemented by only the most abundant and most easily found invertebrate types which include Coleoptera, Homoptera, miscellaneous Arachnida, millipeds, and centipedes. The downy woodpecker retains its food coactions by feeding exclusively upon invertebrates.

The barred owl was the only predator present throughout the year. Because of its role as a coactee in the check on the abundance of mice, shrews and, to a certain extent, on other birds, it may be regarded as a major perennial influent in the associes. Barred owl pellets were surprisingly few in number in any one place. But, because of their presence at various sections throughout the forest, one might be led to believe that their nightly hunting was accompanied by much activity. Roosting holes were used only for shelter during the daylight hours. The pellets in all cases showed that 95 per cent of the total food for the year was made up of the wood mouse, *Peromyscus leucopus noveboracensis* (Fischer), and the short-tailed shrew, *Blarina brevicauda* (Say). The discovery of indigo bunting and warbler feathers in the pellets (especially during May and June) may account for one or two disappearances of indigo bunting young. In all cases the nests were slightly torn, and the adults had vanished. Williams (1936) reported similar findings. Fisher (1893) recorded that the barred owl was also an eater of insects.

In an investigation of the food of several owls in central Illinois, Cahn & Kemp (1930) made a study of the barred owl pellets collected in Brownfield Woods, Illinois, and Turkey Run State Park, Indiana, during the winter of 1925. Brownfield Woods, which resembles Trelease Woods, lies one and one-half miles northwest of Trelease Woods and is also owned by the University of Illinois. Of the 58 pellets collected, 79 per cent of the total food consisted of mammals. *Microtus ochrogaster* (Wagner) (not found in the forest) and *Peromyscus leucopus noveboracensis* (Fischer) made up 55% of the total. The cottontail (*Sylvilagus floridanus mearnsii* (Allen)) contributed 15%, the northern gray squirrel (*Sciurus carolinensis leucotis* Gmelin) 6% and the opossum

(*Didelphis virginiana* Kerr) 3%. Of the bird remains, the following were found in the pellets: woodpecker, 3%; eastern robin (*Turdus m. migratorius*) 6%; eastern crow (*Corvus b. brachyrhynchos*) 3%; eastern mourning dove (*Zenaidura macroura carolinensis*) 3%; and domestic fowl (remains in 5 pellets), 3%. The remaining 3% of the food was made up of the common leopard frog (*Rana pipiens* Schreber).

Stomach analyses of the birds under observation were compared with those reported by earlier investigators (Table 9). The food coactions for the total year had to be estimated since, in most cases, the contents of a large number of stomachs were given with no reference to time or place. A comparison with Table 8 shows a fairly uniform correspondence with the total yearly foods of the birds in question.

FOOD NEXES

The overlapping of nesting territories might engender the assumption that there is an appreciative amount of competition for suitable territories which provide food. Even within a given society, however, the apparent overlapping of territories did not necessarily bring about competition between species because of particular physiological adaptations. An example may be cited in the case of the downy woodpecker and the red-headed woodpecker. During the aestival period, the downy woodpeckers were most active in the smaller trees and high shrubs, and in the hiemal aspect, in the standing weed stalks. The red-headed woodpeckers visited the larger trees while in the forest, and on leaving, during the serotinal, autumnal and part of the hiemal period, invaded the surrounding fields, where they changed their coactive activities. They were seen, for instance, catching flying-insects instead of working into trees for their food, bringing out the variation in physiological adaptations of two members of the same group.

The tufted titmouse was a competitive coactee of the white-breasted nuthatch and brown creeper during the hiemal period. Even then, the tufted titmouse used two hectares per individual, whereas the white-breasted nuthatch and brown creeper used only one hectare per individual.

The flycatchers were entirely insectivorous coactees in that they caught mostly flying insects. Their only competitors, and they were of little consequence because of the greater abundance of insects and other food during these periods, were some of the warblers, including the Myrtle warbler (*Dendroica coronata*), redstart (*Setophaga ruticilla*) and others during the spring and fall migrations.

A general survey of the avian populations shows that each species belongs to an individual society, either a specific layer society during the nesting season or a more general community during the other seasons of the year—based on the abundance and availability of the food supply and upon the climatic factors, wind exposure, temperature and snow. By means of food charts, a comparison has been made of the aestival and hiemal food nexe.

Figure 12 clearly shows the dependency of the birds

TABLE 9. Some reports of stomach analyses in the literature.

| Species | Number of stomachs | GENERAL YEARLY FOOD PERCENTAGE | | | | | | | | | | | | Author | |
		Vegetable	Lepidoptera	Coleoptera	Hemiptera	Diptera	Hymenoptera	Orthoptera	Homoptera	Arachnida	Miscellaneous	Mice and Shrew	Birds		
Indigo Bunting	18	....	67	29	....	....	trace	....	....	....	....	....	....	Forbes	1883
Wood Thrush	41	64	12	17	3	trace	9	trace	....	....	....	....	....	Henderson	1927
Maryland Yellow-Throat	3	....	80	8	5	4	....	....	....	....	....	....	....	Forbes	1883
Cardinal	498	71	5	10	4	....	.9	6	....	....	....	....	....	Henderson	1927
Red-eyed Vireo	569	14	32	....	15	....	10	....	....	....	28	....	....	Henderson	1927
Wood Pewee	359	1	12	14	5	29	28	3	....	2	2	....	....	Henderson	1927
Downy Woodpecker	723	13	....	30	....	....	21	....	....	....	26	....	....	Henderson	1927
Red-headed Woodpecker	443	66	....	20	....	....	6	3	....	....	....	....	....	Henderson	1927
White-breasted Nuthatch	34	41	....	....	....	....	....	....	....	....	52	....	....	Henderson	1927
Barred Owl	2157	....	(24 other mammals)								....	55	18	Cahn	1930
Starling	2157	43	....	....	....	....	....	....	....	....	57	....	....	Henderson	1927
Tufted Titmouse	?	34	(summer diet)								67	....	....	Gillespie	1930
Crested Flycatcher	265	6	21	16	....	....	2	15	....	....	39	....	....	Henderson	1927
Yellow-billed Cuckoo	155	....	50	....	....	....	....	....	....	....	50	....	....	Weed and Dearborn 1903
R. Throated Hummingbird	59	6	(94% animal)								....	....	....	Henderson	1927
Cowbird	544	77	(23% animal)								....	....	....	Henderson	1927

upon the plants within the community during the hiemal period. The invertebrates are, for the most part, in hibernation, or are wintering as eggs or larvae and are inactive. They are eaten principally by such birds as the robin, tufted titmouse, cardinal, and starling. These birds expose numerous hibernating adult and larval invertebrate types by scratching up the duff of the forest floor, creating a surface reaction that was initiated by a feeding coaction. The remaining groups, which include the woodpeckers, brown creepers and white-breasted nuthatches, glean Arachnida, scale insects, and Coleoptera from the surface of the trees; or as in the case of the woodpeckers, institute a reaction by digging into rotten wood—another instance of stimulation by a food coaction.

There is not sufficient invertebrate life in the hiemal period to warrant complete animal diets for the birds. As indicated in the hiemal food chart, all except the brown creeper (which is insectivorous) depend to a great extent upon plant materials. The junco and tree sparrow feed largely upon grass and weed seeds. Wild fruits and grains are eaten by the cardinal, robin, starling, tufted titmouse, and even the red-headed woodpecker and white-breasted nuthatch. These hiemal food coactions of birds are in part responsible for the sowing of such plants as trumpet weed, cherry, virginia creeper, and many others that are early members of forest succession. Of the other coactees of the food chain, the fox squirrel, rabbit and deer mouse feed on bark, roots and acorns. These animals in turn undergo the predatory coaction of the barred owl.

The aestival food nexe illustrated in Figure 12 is almost a reversal of the hiemal food nexe. In the aestival period, the insects come out of hibernation and move to their separate niches in the community.

The food of these various insect types is primarily plants and plant products. The mammals (rabbits, fox squirrels, and deer mice) feed on much the same plant materials during this period as they do during the hiemal period except for the addition of green leaves. As in the hiemal period, these animals are preyed upon by the barred owl. The insects utilize the plants as their chief source of food: lepidopterous larvae live on the green leaves; Diptera, Homoptera, and Hymenoptera find food in the leaves, sap, and juices of plants and flowers; Coleoptera feed chiefly on dead organic decay, leaves and also on other insect types. Birds, in turn, feed upon masses of insect forms, both adult and larval. The Maryland yellow-throat, red-eyed vireo, wood thrush, and tufted titmouse feed on the adults and larvae of Diptera, Lepidoptera, Homoptera, Coleoptera, Hymenoptera, and Arachnida. The downy woodpecker, red-headed woodpecker, and white-breasted nuthatch live on such forms as Lepidoptera, Diptera, and wood borers. The flycatchers concentrate on the flying types, mostly Diptera, Hemiptera, Orthoptera, and Coleoptera.

When studied from the seasonal aspect, the nexes within the community indicate a decided cycle. In the elm-maple associes, the avian population, as a whole, does not depend upon any one specialized type of food throughout the year, but rather it tends to choose the most abundant type, whether it be plant or animal. This adaptability of the birds to their food requirement is the factor which most easily explains the instability of an avian population. Fluctuations in numbers of the avian population are at times extreme; considerable fluctuation is exhibited even in the hiemal population. Avian population, then, must be considered as an important influent element which varies its effects on the community in accord with the seasonal phenomena.

FIG. 12. Food cycle charts for hiemal and aestival periods.

SEASONAL LIST OF BIRDS

The common and scientific names and the order of listing are those adopted by the American Ornithologists' Union Check List of North American Birds, Fourth Edition, 1931. A total of 105 species were recorded for the elm-maple forest.

Perennial Residents

Eastern Bob-white........*Colinus virginianus virginianus* (Linnaeus)
Northern Barred Owl......*Strix varia varia* Barton

Northern Flicker..........*Colaptes auratus luteus* Bangs
Red-bellied Woodpecker...*Centurus carolinus* (Linnaeus)
Red-headed Woodpecker...*Melanerpes erythrocephalus* (Linnaeus)
Eastern Hairy Woodpecker.*Dryobates villosus villosus* (Linnaeus)
Northern Downy Wood-
    pecker................*Dryobates pubescens medianus* (Swainson)
Northern Blue Jay........*Cyanocitta cristata cristata* (Linnaeus)
Eastern Crow.............*Corvus brachyrhynchos brachyrhynchos*
    Brehm
Tufted Titmouse..........*Baeolophus bicolor* (Linnaeus)
White-breasted Nuthatch..*Sitta carolinensis carolinensis* Latham
Carolina Wren............*Thryothorus ludovicianus ludovicianus*
    (Latham)

Starling.................*Sturnus vulgaris vulgaris* Linnaeus
Eastern Cardinal.........*Richmondena cardinalis cardinalis* (Linnaeus)
Red-eyed Towhee.........*Pipilo erythrophthalmus erythrophthalmus* (Linnaeus)

Hiemal Residents

Eastern Red-tailed Hawk..*Buteo borealis borealis* (Gmelin)
Northern Red-shouldered Hawk...............*Buteo lineatus lineatus* (Gmelin)
American Rough-legged Hawk...............*Buteo lagopus s.johannis* (Gmelin)
Ring-necked Pheasant.....*Phasianus colchicus torquatus* Gmelin
Northern Blue Jay........*Cynaocitta cristata cristata* (Linnaeus)
Brown Creeper...........*Certhia familiaris americana* Bonaparte
Winter Wren............*Nannus hiemalis hiemalis* (Vieillot)
Eastern Robbin...........*Turdus migratorius migratorius* Linnaeus
Eastern Golden-crowned Kinglet..............*Regulus satrapa satrapa* Lichtenstein
Eastern Goldfinch........*Spinus tristis tristis* (Linnaeus)
Slate-colored Junco.......*Junco hyemalis hyemalis* (Linnaeus)
Eastern Tree Sparrow.....*Spizella arborea arborea* (Wilson)
Eastern Song Sparrow.....*Melospiza melodia melodia* (Wilson)

Seasonal Migrants

Sharp-shinned Hawk......*Accipiter velox velox* (Wilson)
Broad-winged Hawk......*Buteo platypterus platypterus* (Vieillot)
Eastern Pigeon Hawk.....*Falco columbarius columbarius* Linnaeus
Eastern Sparrow Hawk....*Falco sparverius sparverius* Linnaeus
Yellow-bellied Sapsucker...*Sphyrapicus varius varius* (Linnaeus)
Yellow-bellied Flycatcher..*Empidonax flaviventris* (Baird and Baird)
Eastern Hermit Thrush....*Hylocichla guttata faxoni* Bangs and Penard
Olive-backed Thrush.....*Hylocichla ustulata swainsoni* (Tschudi)
Gray-cheeked Thrush.....*Hylocichla minima aliciae* (Baird)
Veery...................*Hylocichla fuscescens fuscescens* (Stephens)
Eastern Ruby-crowned Kinglet..............*Corthylio calendula calendula* (Linnaeus)
Yellow-throated Vireo.....*Vireo flavifrons* Vieillot
Blue-headed Vireo........*Vireo solitatius solitarius* (Wilson)
Eastern Warbling Vireo....*Vireo gilvus gilvus* (Vieillot)
Black and White Warbler...*Mniotilta varia* (Linnaeus)
Prothonotary Warbler.....*Protonotaria citrea* (Boddaert)
Golden-winged Warbler....*Vermivora chrysoptera* (Linnaeus)
Orange-crowned Warbler...*Vermivora celata celata* (Say)
Nashville Warbler........*Vermivora ruficapilla ruficapilla* (Wilson)
Eastern Yellow Warbler....*Dendroica aestiva aestiva* (Gmelin)
Magnolia Warbler........*Dendroica magnolia* (Wilson)
Cape May Warbler........*Dendroica tigrina* (Gmelin)
Black-throated Blue Warbler..............*Dendroica caerulescens caerulescens* (Gmelin)
Myrtle Warbler..........*Dendroica coronata* (Linnaeus)
Black-throated Green Warbler..............*Dendroica virens virens* (Gmelin)
Cerulean Warbler........*Dendroica cerulea* (Wilson)
Blackburnian Warbler.....*Dendroica fusca* (Müller)
Chestnut-sided Warbler....*Dendroica pensylvanica* (Linnaeus)
Bay-breasted Warbler.....*Dendroica castanea* (Wilson)
Black-poll Warbler........*Dendroica striata* (Forster)
Oven-bird...............*Seiurus aurocapillus* (Linnaeus)
Northern Water-Thrush...*Seiurus noveboracensis noveboracensis* (Gmelin)
Louisiana Water-Thrush...*Seiurus motacilla* (Vieillot)
Connecticut Warbler......*Oporornis agilis* (Wilson)
Northern Yellow-throat....*Geothlypis trichas brachidactyla* (Swainson)
Wilson's Warbler........*Wilsonia pusilla pusilla* (Wilson)
Canada Warbler.........*Wilsonia canadensis* (Linnaeus)
American Redstart.......*Setophaga ruticilla* (Linnaeus)
Eastern Red-wing........*Agelaius phoeniceus phoeniceus* (Linnaeus)
Baltimore Oriole.........*Icterus galbula* (Linnaeus)
Rusty Blackbird.........*Euphagus carolinus* (Müller)
Scarlet Tanager.........*Piranga erythromelas* Vieillot
Rose-breasted Grosbeak...*Hedymeles ludovicianus* (Linnaeus)
Eastern Purple Finch.....*Carpodacus purpureus purpureus* (Gmelin)
Eastern Chipping Sparrow..*Spizella passerina passerina* (Bechstein)
White-crowned Sparrow...*Zonotrichia leucophrys leucophrys* (Forster)
Gambel's Sparrow........*Zonotrichia leucophrys gambeli* (Nuttall)

White-throated Sparrow...*Zonotrichia albicollis* (Gmelin)
Eastern Fox Sparrow.....*Passerella iliaca iliaca* (Merrem)
Swamp Sparrow.........*Melospiza georgiana* (Latham)

Aestival Residents

Eastern Mourning Dove...*Zenaidura macroura carolinensis* (Linnaeus)
Yellow-billed Cuckoo......*Coccyzus americanus americanus* (Linnaeus)
Black-billed Cuckoo.......*Coccyzus erythropthalmus* (Wilson)
Ruby-throated Humming-bird..................*Archilochus colubris* (Linnaeus)
Northern Crested Fly-catcher................*Myiarchus crinitus boreus* Bangs
Eastern Wood Pewee......*Myiochanes virens* (Linnaeus)
Wood Thrush............*Hylocichla mustelina* (Gmelin)
Red-eyed Vireo..........*Vireo olivaceus* (Linnaeus)
Maryland Yellow-throat...*Geothlypis trichas trichas* (Linnaeus)
Bronzed Grackle.........*Quiscalus quiscula aeneus* Ridgway
Eastern Cowbird.........*Molothrus ater ater* (Boddaert)
Indigo Bunting..........*Passerina cyanea* (Linnaeus)
Dickcissel................*Spiza americana* (Gmelin)

Incidental Visitors

Great Blue Heron.........*Ardea herodias herodias* Linnaeus
Eastern Green Heron......*Butorides virescens virescens* (Linnaeus)
Black-crowned Night Heron................*Nycticorax nycticorax hoactli* (Gmelin)
Cooper's Hawk...........*Acanthis linaria linaria* (Linnaeus)
King Rail................*Rallus elegans elegans* Audubon
Virginia Rail.............*Rallus limicola limicola* Vieillot
Sora...................*Porzana carolina* (Linnaeus)
American Woodcock......*Philohela minor* (Gmelin)
Eastern Whip-poor-will....*Antrostomus vociferus vociferus* Wilson
Eastern Nighthawk.......*Chordeiles minor minor* (Forster)
Chimney Swift...........*Chaetura pelagica* (Linnaeus)
Purple Martin...........*Progne subis subis* (Linnaeus)
Carolina Chickadee.......*Penthestes carolinensis carolinensis* (Audubon)
Common Redpoll.........*Acanthis linaria linaria* (Linnaeus)

SUMMARY AND CONCLUSIONS

1. The birds of the elm-maple associes were characterized by continuous fluctuations in numbers throughout the various aspects of the community.

2. The vernal and autumnal peaks corresponded with the two main insect peaks. These maximum levels were reached during 1934 and 1935 when the average mean daily temperature registered 59 to 61° F.

3. The local movements of the birds in the community from forest to forest edge were in part caused by changes in weather factors, such as prevailing winds and temperature. These local movements were most pronounced during the hiemal period, when cold west or southwest winds drove the birds to the east forest edge for protection. On the other hand, the appearance of insects that had been hibernating on the surface of the ground layer during warm periods stimulated variable movements in the bird populations.

4. The aestival aspect was one of comparative stability of the nesting population. It was marked by territorial coactions—competition for suitable mates, nest building and territorial space within the community for the care and feeding of the young as well as for the adults.

5. The methods of censusing (cruising and sampling) were on a quantitative basis, and the results, other than for the breeding season, are relative in

character. There was considerable movement from place to place and some birds were doubtless counted more than once during a particular censusing operation.

6. There were vertical limitations of territories to layer societies of shrubs, trees, etc., as well as horizontal limitations within a layer society.

7. There is a limitation as to available sites within a layer society depending upon the structural adaptations of the species and the physical habitat.

8. The climax association had few nesting species. The major nesting population was confined to the developmental communities.

9. The population density for the nesting species was 0.3 hectares (0.74 acres) per pair in 1934 and 0.32 hectares (0.79 acres) per pair in 1935.

10. The coactive activity of the birds within the community was found to change with the seasonal aspects. The most abundant insect and plant foods of each aspect were selected by the birds (Table 8).

11. There was a reversal of the food nexes of the aestival and hiemal periods (Fig. 12).

12. The avian population is an important influent element which varies its effects on the community in accord with the seasonal phenomena.

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